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A FIELD STUDY OF THE SLENDER GLASS LIZARD, *OPHISAURUS ATTENUATUS*, IN NORTHEASTERN KANSAS

By

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Nearly a year after initiating ecological studies on the University of Kansas Natural History Reservation (UKNHR) in July 1948, I saw for the first time a slender glass lizard (*Ophisaurus attenuatus*) on the area. As in most other areas where the species occurs, it was rare and few records of it accrued with the passing years for nearly a decade. However, as ecological succession progressed on the UKNHR with protection (after 1948) from cultivation, grazing, and other direct and indirect effects of man's activities, it became evident that the habitat changes were benefitting the glass lizard. Its numbers increased as did the area occupied. Nevertheless, because of relatively slow growth and low reproductive potential in the glass lizard compared with other small vertebrates, the population increased gradually, and seemed to reach peak numbers about 18 years after the policy of protection had initiated rapid successional change. At that stage much interest and effort were directed to the study of glass lizards. On one occasion in 1966, 70 individuals were captured in a single day. Although numbers have gradually declined during the second half of the 35-year observation period, a total of 2116 slender glass lizards has been recorded 3353 times (including recaptures of marked individuals). All of these sightings were on UKNHR, on the Rockefeller Experimental Tract, or near the boundaries of these two contiguous areas owned by the University of Kansas.

Over the period spanned by this field study, interest in lizard ecology has

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greatly increased, as indicated by the appearance of two recent books under that title. Many field studies on lizards have been made and published upon, and constitute important contributions to ecology in general. However, in these studies, certain types of iguanids, teiids, and other lizards that live in open habitats and can be observed or captured with relative ease have been given the most attention. More secretive types, including those of the family Anguidae to which *Ophisaurus* belongs, have remained almost unknown ecologically. Published information concerning the behavior and natural history of *O. attenuatus* is meager and mostly anecdotal. The most extensive account (Trauth, 1984) was based upon 17 field records plus 39 museum specimens. The late Paul Anderson (1965), in many years of intensive field work on the Missouri herpetofauna, collected only five. The late Dr. E. H. Taylor, well-known herpetologist and longtime Kansas resident, told me (pers. comm.) that he had seen only about a dozen of these lizards in his lifetime. My objective in undertaking the present study was to find out as much as possible concerning the natural history of the species.

METHODS AND MATERIALS

Field observations began in 1949 and has continued through 1988. During the early stages of this study, slender glass lizards were found by chance during the course of other activities, and each was examined, measured, weighed, and marked. Most were captured in the tall grass of a former pasture. Hunting them was found to be rewarding at certain times in warm humid weather. They were especially active after brief showers and were also found to have more or less regular periods of activity in the morning and late afternoon. At these times I would occasionally flush a glass lizard and, as it darted away, often for a distance of 2–5 m, I would follow its course by the rapidly waving tops of tall grass. Then, approaching slowly and stealthily toward the point where motion was last seen, I frequently was able to see the lizard, or a small section of its body or tail, at the base of the grass stems. Captures were made by a sudden forward lunge of 1–3 m while, at the same time, aiming for the head and forebody of the lizard in order to pin it against the substrate and also avoid contact with the fragile tail. Often if a lizard flushed a second time during an approach, or if it dodged the capture attempt, it would then dart away farther than it had the first time. After one or more stalking attempts, the lizard would often elude further pursuit by disappearing into a burrow or beneath the surface litter or under a thick bush.

Success in hunting slender glass lizards was improved when two or more persons collaborated as a team and walked parallel to one another (2–3 m apart) during the search. When a lizard was flushed, one person (the catcher) stood motionless while his helper(s) moved ahead to outflank the lizard; then the helper would approach the lizard from the front and attempt to drive it back within reach of the catcher. One of my collaborators, Donald M. Troyer, became an expert at capturing glass lizards as a result of long practice and natural talent.

Although the majority of records were of slender glass lizards captured by hand, many also were captured in wire funnel traps set for snakes on the same area (Fitch, 1951). The trap captures were seasonally biased (most occurred in May, the breeding season) and were predominantly adult males; however, in the latter years of the study the trap captures became increasingly important as woody vegetation progressively dominated the study area, rendering capture by hand difficult.

The system of marking involved clipping ventral scales at the edge of the lateral fold, three scales from each lizard (see Fig. 1). The anteriormost of the three scales constituted a base mark at one of several predetermined positions from which a count began: "Front Left" near the anterior end of the lateral fold, or "$^1/_3$ Left," "$^1/_2$ Left," "$^2/_3$ Left," or any one of the corresponding positions on the right side of the body. The remainder of the formula indicated the positions of the two other clipped scales with respect to the base mark, i. e., "$^1/_3$ Left 2–4" for the first lizard at the beginning of a series and "$^1/_3$ Left 33–35" at the end for the last one. Counts were not extended beyond the mid-thirties because of time and tedium involved in long counts and the increased chances for error. At least one scale was always left unclipped between the base mark and the next clip. Likewise, at least one scale was always left between the second and third scales clipped in a series. Marking involved thoroughly excising the scales. After healing had occurred, the scars were still conspicuous as notches along the lateral fold. After marking by scale-clipping a lizard would become limp and passive, a behavior that might be construed as death-feigning.

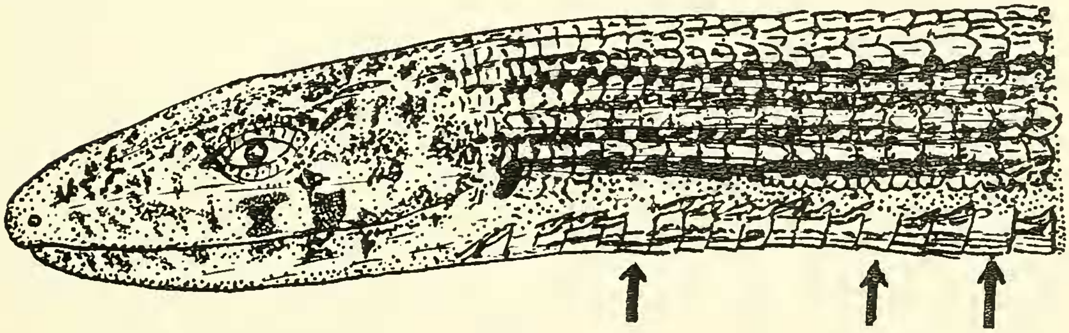

Fig. 1. Method of marking glass lizards by clipping scales along the lateral fold. The formula, Front Left 8–11, is illustrated.

Snout-vent length (SVL) was measured to the nearest millimeter by stretching the lizard to its full length while pressing it against a ruler. Tail length was measured in like fashion but involved exceedingly slow and cautious manipulation to induce the animal to straighten its tail momentarily against a ruler or stretched tape, with due regard for the tail's fragility.

Original and regenerated parts of the tail were measured separately. Head width was recorded. Weight was recorded, usually by suspending the animal directly from the hook of spring scales after it had been sufficiently calmed by careful handling. Broken tails were weighed separately from the lizard itself. Color and pattern were noted in each individual, especially on the head and dorsolateral area. Sex was noted. The standard procedure for sexing snakes of inserting a blunt probe into the base of the tail to demonstrate the presence of a hemipenis was not successful for slender glass lizards because of the presence of a sac-like cloacal caecum behind the anus and because of the shortness of the hemipenis. In a male, partial or complete eversion of the hemipenes could often be accomplished by pressing lightly on the ventral side of the tail near its base, with a slight twisting motion. If the hemipenis, or even its outer edge, came into view after several trials, this fact was noted and the individual was definitely identified as a male. If no indication of a hemipenis could be found, the lizard was presumed a female, but this assignment was by no means certain. Males could also be recognized by their relatively broad heads and by white flecks on the anterior part of the dorsolateral area that became more prominent with increasing age.

My field study centered on UKNHR and especially on its northwestern quarter-section in House Field and the adjacent areas of Horse Field, Picnic Field, Hole Field, and Vole Field. Dozens of named landmarks based on natural features such as trees and rocks (shown on detailed maps and in aerial photographs) made it possible to locate points with precision. A grid of small mammal traps marked by metal stakes at 50-foot (15.2 m) intervals over most of the area also facilitated orientation and location of capture points. This study area is on gently sloping land at the head of a small valley draining into an unnamed intermittent creek, a tributary of Mud Creek, which in turn is a tributary of the Kansas River. The House Field area probably was mostly bluestem prairie under original conditions. It was heavily overgrazed in the late 1800s and early 1900s, was sown to the non-native *Bromus inermis* (probably in the 1930s), and was protected from grazing after 1948, resulting in revival of grasses followed by encroachment of woody vegetation. Descriptions and history of the area have been set forth in detail in earlier publications (Fitch, 1952; Fitch and Shirer, 1971; Fitch and Hall, 1978). A separate nearby study area, Quarry Field, situated on a flat hilltop 230 m north of House Field, was similar to this area in its habitats and history. A small percentage of the glass lizard records accumulated came from other miscellaneous areas including the upland prairie of the Rockefeller Experimental Tract, and the Road Field-High Field area (eroded upland oldfield sown with seeds of native prairie tall grasses) of northeastern UKNHR, and a few more remote locations.

Where the data presented in this paper include mean values, these are accompanied by standard errors if sufficient series were available.

RESULTS AND DISCUSSION

Description. *Ophisaurus attenuatus* is a slender, elongated legless lizard, characterized by a tail much longer than its body, keeled dorsal scales, a long and slightly depressed snout, a countersunk lower jaw, a deep lateral fold with granular scales for the full length of the body, eyelids and girdles, and body color tan with a black middorsal stripe and several narrow black stripes on each side.

Scales on top of the head are flattened plates. From front to rear there is a median rostral and just behind it a much smaller postrostral bordered on either side by a preinternasal. The paired postinternasals are rectangular, in contact anteriorly and divergent posteriorly along the anterior borders of the large median frontonasal. The ovate frontal is the largest plate by far. Anteriorly it contacts the paired prefrontals on either side. Laterally the frontal is bordered by three supraoculars on each side; the pear-shaped interparietal between winglike parietals narrowly contacts the interoccipital. On each side a postfrontal in a notch between the frontal, parietal, and interparietal separates the fourth supraocular from the frontal. There are six supracanthals on each side forming a longitudinal ridge on the dorsolateral aspect of the snout, with a row of canthals below them. There are many small temporal scales, arranged in about four irregular transverse and four longitudinal rows. On the side of the head there are an upper and lower postnasal, about eight loreals, two preoculars, six suboculars, 11 supralabials, and one lorilabial intercalated between the eighth supralabial and the suboculars. On the midline of the chin there are a median mental and anterior and posterior postmentals. There are about 10 pairs of infralabials and a similar series of sublabials below them. There are four pairs of enlarged chin shields and several rows of small crescentic gulars. Dorsal body scales are heavily keeled and tend to be rectangular on the back and rhomboid on the sides in regular transverse and longitudinal rows (numbering about 121 and 18, respectively). Ventral body scales are smooth and flat in about 117 transverse and 12 longitudinal rows (including on each side a row of half-sized scales bordering the lateral fold). Ventral scales tend toward hexagonal shape, with the width somewhat greater than the length. On the lateral fold scales are minute and granular and lack osteoderms. These scales vary in size and are not in regular rows; there are about three scales in a transect across the lateral fold, which is almost scaleless on its lower half.

The following description of color and pattern is that of an old adult male. The top of the head is darker than the body and has no distinct marks anteriorly. There are irregular black spots, some faint, on the frontal, parietals and interparietals, and posterior supraoculars, and there are white markings of irregular size and shape, centering along the sutures between these scales. The dorsum, 10 scale rows wide, is tan brown except for the two middorsal rows which are mostly black but paler and brown along their inner edges for the length of the body and tail. There are irregular and incomplete transverse marks across the dorsum, each involving a distance of two to three scale lengths, and each transverse mark is separated from the next anterior or posterior by about the same distance. A transverse mark consists of several small black and white spots, each spot somewhat less than the size of a scale and irregular in size, shape, and arrangement. Each black marking tends to be within a single scale whereas the white markings tend to center on the contact lines between scales. The transverse markings dwindle posteriorly, being scarcely noticeable behind midbody, and always absent from the tail. The sides are mostly black, but with white marks on every scale; the darkened area includes the four lowest scale rows and part of the fifth. In the fourth row each scale has a pale dot, and these form a dotted line. Between the fourth and fifth rows there is an edging of white which forms a narrow line for the length of the body and tail, but has occasional breaks and uneven edges. White edges at the contacts between rows two and three form another similar narrow light line paralleling the upper one. The face has a speckled appearance as almost every scale on the side of the head is marked with black on a whitish or pale brown background. The black marks occupy a somewhat greater extent than the intervening pale areas and are rather irregular (often angular) in shape. Brownish and unmarked scales include the rostral, nasal, and first two pairs of supralabials and infralabials. The chin is white except for small black marks on the infralabials and sublabials. On the ventral surface of the body, the first and second lateral scale rows have dark brown marks on each scale, that are narrowly separated or in contact, forming a faint ventrolateral line. Scales of the second row each have a smaller dark mark along the medial edge, and some of these marks have smaller counterparts along the adjacent edges of the third row. Collectively, all these marks form a second fainter ventrolateral line. At contacts between the third and fourth ventral row there is a slight darkening with the suggestion of a third stripe.

In an adolescent female the face and dorsal surface are tan. There are seven longitudinal black stripes extending the length of the body and tail. Each stripe centers along the line of contact between two scale rows. Both the middorsal and dorsolateral stripe slightly exceed the width of a scale row, but the dorsolateral stripe is more intense, with sharper edges. The midlateral stripe is a little less than one scale wide and is separated from the dorsolateral stripe by a narrow (less than half a scale width) white or pale tan line. A sublateral stripe is narrower than the midlateral stripe, is less than half a scale wide, and is separated from the midlateral stripe by a narrow white line similar to that between the dorsolateral and midlateral black stripes. On the edge of the ventral surface there are two brown stripes on each side; the outer one lies along the contact between first and second scale rows and the inner one (less well-defined) lies along the contact between the second and third rows. From the subocular region back across the cheek and side of the neck, scales are pale, almost white, with dark brown marks which tend to be arranged in several vertical bars. There are faint black marks on top of the head on the frontal, parietals, interparietals, and occipital. There are occasional black dots on the tan dorsolateral area one scale row medial to the dorsolateral stripe. These sometimes appear on several successive scales, forming a broken line, and on the tail they become continuous forming an additional heavy black stripe on each side. The regenerated tail has no markings and is dark amber dorsally and ivory ventrally. The iris is golden.

Adult males differ from females in having the face and the dorsolateral area, especially its anterior part, marked with irregular black and white areas or flecks, which become more extensive and better defined as the individual ages (Plates I and II). Juveniles are like adult females in having the dorsolateral area pale brown and unmarked, but in having dark facial markings faint and poorly defined (Plate I).

Sexual dimorphism. Determination of sex is usually straightforward in old adults on the basis of coloration, but the external differences may be subtle in young adults or immatures. Exposing at least one edge of the hemipenis when possible permitted definitive identification as a male; if the hemipenis could not be found, sex remained undetermined with only tentative identification as a female.

In adult males, white flecks mark the tan dorsolateral area, especially its anterior half. In some old adults, the white flecks are large and numerous and tend to be arranged in transverse bands with unmarked areas between. Black dots or edges on the same scales bearing white impart a "salt and pepper" effect. In recently matured males of 190–210 mm SVL, the dorsolateral area is pale tan, unmarked, or marked with an occasional black dot, as in females; however, close inspection of these individuals reveals occasional traces of the white flecks along the outer edges of the dorsolateral areas. Although the white dorsolateral flecks are normally lacking in females, there are rare exceptions. Certain large, old females have the flecks well developed, and such individuals might be erroneously sexed as males.

The intact tail averages about 4% longer in adult males than in adult females, but there is individual overlap (Fig. 2). Also, the head is wider in adult males than in adult females of similar SVL. This widening of the head in males is associated with well developed temporal muscles and with the capability to deliver a hard bite. In this species and other kinds of lizards in which there is male rivalry and fighting, the males tend to have swollen jaw muscles. The head is relatively much wider in hatchlings than in adults, and as allometric growth progresses, the body grows faster than the head. Also, there is allometric growth within the head itself, resulting in subtle changes in its shape; for instance, the eye becomes relatively smaller, whereas the jaw muscles become larger. In hatchlings, the head width averages 7.46% of SVL, but that percentage gradually decreases as growth proceeds. In young that have doubled in length since hatching, an average sexual difference in head width is discernible, with male head width averaging 5.5% of SVL vs. 5.34% in females. Heads are narrower in preadolescents between 160 and 170 mm SVL, averaging 5.25% of SVL in males and 5.02% in females. From that stage onward, sexual difference in head width increases, and the width is relatively greater in large adult males (averaging up to 5.78% of SVL) as compared to large adult females (averaging down to 4.73% of SVL). For comparisons, see Fig. 3.

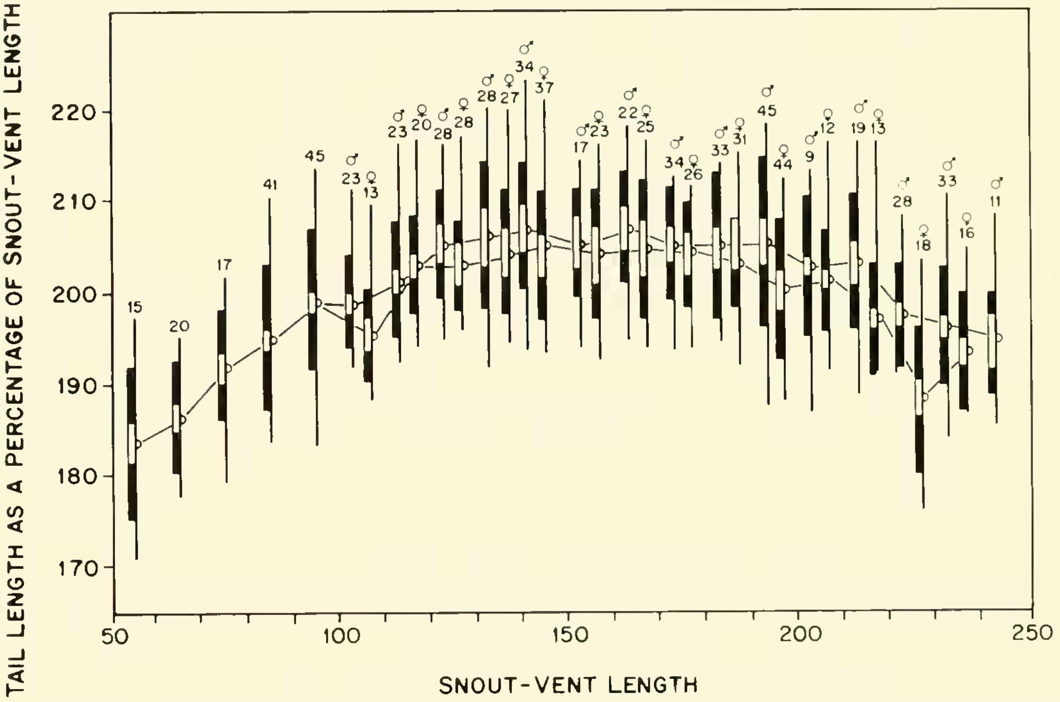

Fig. 2. Tail length as percentage of snout-vent length in glass lizards having tails intact. Mean, standard error, standard deviation, and range are shown for each sample. Number of lizards is at top of column.

History and relationships. The genus *Ophisaurus* is ancient and widespread with 12 living species (Holman, 1971a, 1971b, 1971c, 1971d, 1971e, 1971f; Palmer, 1987). Four fossil species are known to span the Cenozoic. The oldest known New World occurrence is a specimen of *O. canadensis* (Holman) from the upper Miocene of Saskatchewan (far to the north of any modern species). All known occurrences, both fossil and modern, are in the Northern Hemisphere and are mostly confined to the temperate zone, but some extend into the tropics. The giant of the genus is *O. apodus* (Pallas) of southeastern Europe and Asia Minor, reported to attain 45 cm SVL; however, the supposedly ancestral Miocene-Pliocene *O. pannonicus* Kormos was larger, perhaps reaching 2 m in total length. *Ophisaurus apodus* and *O. koellikeri* (Günther) of western Morocco are alike in retaining rudiments of hind limbs, but *O. koellikeri* is distinctive in lacking an external ear opening. *Ophisaurus gracilis* (Gray) of the eastern Himalayas and Burma and *O. wegneri* Mertens of Sumatra are alike in having light blue spots on the body, but *O. gracilis* has coarser scalation with 88–84 transverse dorsal scale rows along the lateral fold and 14–16 longitudinal rows, as compared with 96 transverse and 18 longitudinal rows in *O. wegneri*. In *O. harti* Boulenger of southern China and Formosa and *O. buttikoferi* (Lidth de Jeude) of Borneo, there are conspicuous transverse blue markings on the body.

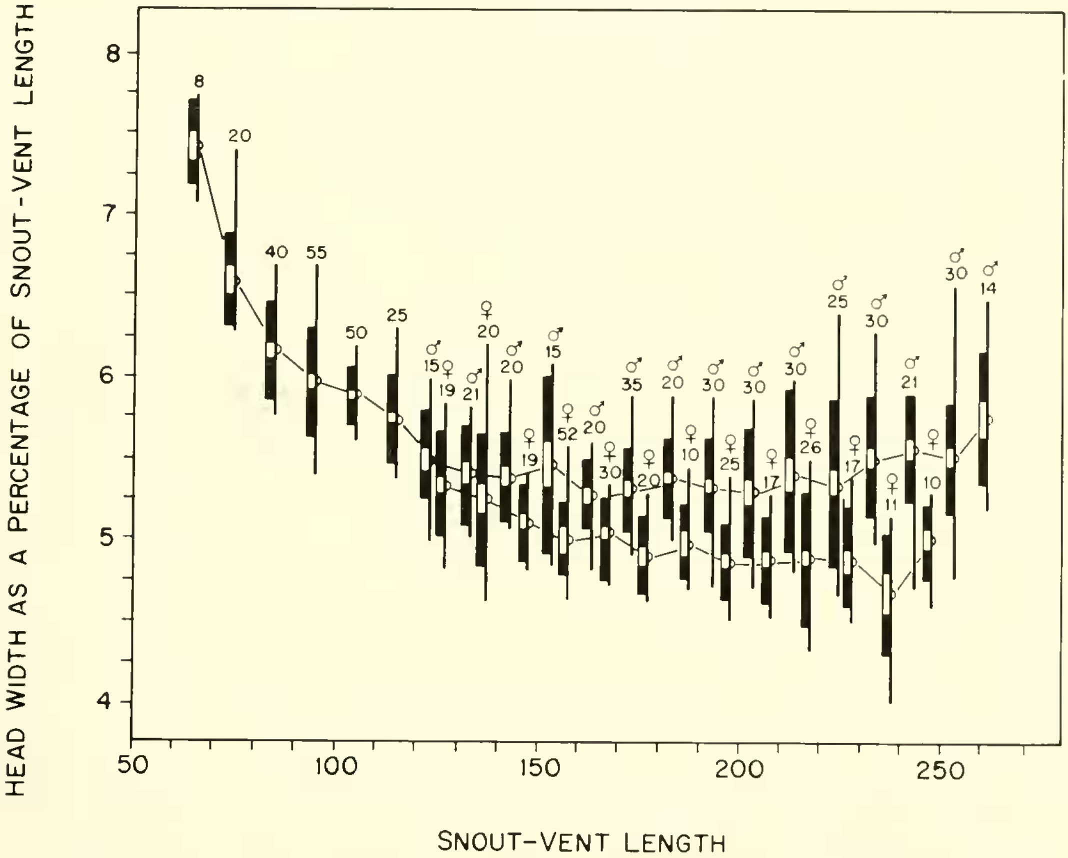

Fig. 3. Ontogenentic and sexual differences in relative head widths. Mean, standard error, standard deviation, and range are shown for each sample. Number of lizards is at top of column.

Six New World species are recognized, of which O. *attenuatus* Cope is the best known and by far the most widely distributed. It differs from other species in its more elongate tail, especially long in *O. a. longicaudus* McConkey, the subspecies east of the Mississippi River, in which the tail is 2.4 or more times SVL, whereas in *O. a. attenuatus*, tail length is less than 2.4 times SVL (McConkey, 1954). *Ophisaurus compressus* Cope occurs in Florida, except the western part, and in the coastal areas of Georgia, South Carolina, and North Carolina. It is a relatively small species (171 mm maximum SVL) and is remarkable in lacking fracture planes in the caudal vertebrae, so the tail is not especially fragile. It has white spots on the edges of the anterior dorsal scales and has no dark markings below the lateral fold. There are no more than 97 scales along the lateral fold. The hemipenis has a ridge on each side of the sulcus running for its entire length. *Ophisaurus ventralis* (Linnaeus) is a medium large species (up to 292 mm SVL) lacking a middorsal stripe and dark markings below the lateral fold. A ridge runs for the entire length of the hemipenial sulcus on its medial side; another ridge on the lateral side of the sulcus extends for only one- fourth its length. *Ophisaurus ceroni* Holman is a small species (181 mm maximum SVL) known from a few specimens from the coastal sand dunes of Veracruz, Mexico. It has a distinct middorsal stripe, but no dark marks below the lateral fold. *Ophisaurus incomptus* McConkey is known from a single damaged specimen from 7 miles south of San Luis Potosí, Mexico. It is like *O. ventralis* in most characters but lacks the vertical white neck bars of that species. The recently described *Ophisaurus mimicus*, from the Atlantic and Gulf coastal plain of the southeastern United States, differs from *O. attenuatus* in markedly smaller size, lack of ventral longitudinal black lines, and relatively larger dorsal scales, in fewer rows (Palmer, 1987).

Ophisaurus differs from some other anguids in being oviparous. Insofar as known, in all species the female stays with her eggs and coils around them during incubation, but females are not aggressive in defense of the clutch (Noble and Mason, 1938). The lateral fold of *Ophisaurus* is shared with the New World gerrhonotine lizards which, however, are placed in a separate subfamily. Although retaining limbs, the gerrhonotines resemble *Ophisaurus* in many traits; some are elongate and serpentiform with limbs reduced; others are lacertiform with more robust bodies and limbs well developed. Some gerrhonotines are viviparous. These lizards are snakelike in shedding their skins entire, whereas *Ophisaurus* sheds its skin in patches.

Sullivan (1987) recently proposed that the genus is diphyletic. *Parophisaurus pawneensis* (Gilmore, 1928) of the middle Oligocene of Colorado is believed to be near the ancestry of the New World species. However, recently collected material of this supposedly ancestral glass lizard has shown that it had well developed limbs and girdle. Sullivan placed the several Old World species of glass lizards in another genus, *Pseudopus*, representing an anguine stock that evolved limblessness earlier, and has been isolated from *Ophisaurus* since the middle Eocene.

General behavior. While some other species seem to be adapted to living in sand dunes, among rocks, or in certain types of forests, *Ophisaurus attenuatus* is associated with tallgrass prairie. During this study, it was observed to be active and agile, moving through the grass with lateral undulations of the body and tail that resembled swimming motions. Depending on conditions of moisture, temperature, and the grass itself, movements could be exceedingly rapid and, at times, a lizard seemed to skim over or through the grass so swiftly that the observer was aware only of a blur of movement and could not even judge the approximate size of the lizard.

Glass lizards searching for prey wandered about over a small familiar area on the surface, but much of the time were inactive, hiding beneath the surface mat of dead vegetation or underground in abandoned burrows of other animals. In addition, lizards hibernated, laid their eggs, retreated from danger, or avoided inclement weather in their burrows. Surface activity was diurnal, crepuscular, or nocturnal, depending on weather conditions. In cool weather of spring and fall, the lizards were most active at midday in full sunshine. In hot weather of midsummer, their activity was concentrated around dusk, and hunting for them was found to be profitable as long as it was light enough to see. On the night of 26 May 1985, in Elk County, Kansas, Joseph T. Collins (pers. comm.) found two slender glass lizards on the road after dark at 2050 and 2110 hours.

Habitat. Tall grass is essential for these lizards. During this study on UKNHR the species thrived and attained maximum numbers on formerly pastured areas that were dominated by the exotic grass *Bromus inermis*; however, when this area was heavily grazed the lizards were exceedingly scarce, and they attained maximum numbers about 18 years after grazing was stopped. By then, the area was considerably altered due to successional changes resulting from the removal of livestock. Brome grass grew in a heavy stand up to 1 m or more in height, and largely crowded out and replaced many of the weedy forbs that were present when the area was grazed. A thick mat of dead grass and other disintegrating plant material covered the ground. Bushes and small trees, growing singly or in clumps, and including sumac (*Rhus glabra*), coralberry (*Symphoricarpos orbiculatus*), dogwood (*Cornus drummondi*), crabapple (*Pyrus ioensis*), wild plum (*Prunus americanus*), honey locust (*Gleditsia triacanthos*), and Osage orange (*Maclura pomifera*), became prominent. Small mammals including mice, voles, moles, and shrews were moderately abundant, but they were much more so during the earlier years of succession. Consequently, the soil was riddled with their tunnel systems, and as numbers declined abandoned burrows became available as escape shelters, hibernacula, and nesting sites for glass lizards.

Other types of grassland also provided suitable habitat. In the northeastern part of UKNHR, a much eroded oldfield area with deep gullies (Road Field–High Field–Low Field) was sown to native prairie tall grasses in 1949 and attained a mixed stand of several grass species (especially little bluestem, *Schizachyrium scoparium*, and switchgrass, *Panicum virgatum*) with clumps of woody vegetation gradually encroaching. Glass lizards became common on this area, but less so than in the House Field vicinity. Immediately to the north of UKNHR on the Rockefeller Experimental Tract, a block of 4.6 hectares of original prairie was managed and maintained with a program of controlled burning in late March (annually or at less frequent intervals). Glass lizards were present on this area (mainly along its edges) but they were not common.

On UKNHR and other places in northeastern Kansas, slender glass lizards were seen from time to time in open woodlands, especially where ground cover was subject to grazing. Numbers were always low in situations having too much shade from the trees and too little ground cover for shelter. Occasional individuals were seen on highways or county roads; this indicated that glass lizards inhabited roadside strips where prairie vegetation persisted as a result of mowing and/or burning.

The tallgrass prairie vegetation on which the slender glass lizard depended for its natural habitat was a fire-type subclimax, ephemeral without periodic burning. Yet the lizard had no obvious adaptations to resist or escape burning. Even if it survived a grass fire by being underground it was rendered highly vulnerable to predation by the complete lack of surface cover after burning and lacked the capacity to disperse to more favorable areas. It responded slowly to favorable conditions by increasing its rate of reproduction. Indeed, it seemed that the species existed somewhat precariously, i.e., in marginal ecotonal stands of tallgrass prairie, an association dependent on recurrent fire, in which streams, gullies, brush patches, woodland edge, or rock outcrops offered some degree of protection from the burning off of all surface cover.

Reproduction. Sexual behavior was observed on 6 May 1964 in a pair of slender glass lizards caught at different places on the preceding day and left overnight in the same container. At 0830 hours, the male repeatedly, but hesitantly, nipped at the female; she showed no response. The male was distracted when he accidentally took wood shavings in his mouth. At 0900 hours, he grasped the female's head diagonally across the occipital region in his jaws. While lying in contact with the female with his vent apposed to hers, he made rhythmic swimming movements with the posterior part of his body from time to time. The female's vent was tightly closed, whereas the male's vent was pressed against the female's with one hemipenis partly everted. The female was not fully pacified, and from time to time she struggled to escape (perfunctorily at first, then more vigorously). She twisted and rolled so that both lizards were lying belly up and, after several such attempts, she broke the male's grip and escaped. The male moved about jerkily and alertly, seemingly searching for the female, and then burrowed into the shavings. When a third glass lizard (one smaller than the original pair and probably a female) was added, the male surfaced, followed it, and caught it by the tail. It escaped after a tussle and, surprisingly, the tail did not break although it was subjected to considerable stress. Later, the male seized the smaller lizard across the forebody, but it turned and bit him on loose skin of the lateral fold. The two writhed, interlocked, and struggled for several minutes until the smaller broke away. On other occasions when a female was introduced into a male's container, or vice versa, the lizards did not respond to each other. Most aspects of behavior seemed to be inhibited by confinement, and the observation of caged lizards was generally unproductive.

Trauth (1984) studied the testicular cycle of the male slender glass lizard in southern Arkansas. Testes were elongate and cylindrical and fully developed in males as small as 150 mm SVL which were found to be sexually mature. Testes were at maximum size from early April to late May at the same time when seminiferous and epididymal tubules were full of spermatozoa. Testicular recrudescence was found to begin in late summer.

Some females of the Kansas population reproduced as adolescents at the age of three years while others postponed sexual maturity until their fourth year. Females were often gravid in June and laid their eggs toward the end of that month or in early July. An attempt was made to determine the ratio of gravid to nongravid females in June; 49 (40%) of those in the 1948–1985 composite sample were judged to be gravid, whereas 75 (60%) appeared not to be gravid. Ratios were not significantly different between size groups as shown by the following figures: 190–199 mm SVL (adolescents, *n* = 36), 33% gravid; 200–214 mm SVL (small adults, *n* = 44), 52% gravid; 215–255 mm SVL (medium and large adults, *n* = 45), 31% gravid. Those suspected of being gravid usually weighed from 9 to 53% more than the average for their male counterparts of the same size at the same time of year. In a few instances, males might have been incorrectly identified as nongravid females when hemipenes could not be discerned. The gravid condition might not have been recognized in some females because their follicles were still too small to distend their bodies noticeably. Females nearly ready to oviposit probably remained in underground nests and, as a result, they were missed in sampling more often than nongravid females. The 40% estimate for gravid females was, therefore, probably too low. The estimate suggested that individual females were on a biennial cycle with about 50% of the female population reproducing in any one year. After the long fast involved in guarding the eggs throughout their incubation period, these females may have needed to spend an entire growing season replenishing their reserves before they were ready to produce eggs again the following season.

Ovarian follicles were small when females emerged from hibernation, and enlarged very rapidly over a period of weeks as shown by the measurements from six dissected females:

23 March 1966	ovarian follicles	1.5 x 1.5 mm	(8 left, 8 right)
23 May 1964	ovarian follicles	5.5 x 5.5 mm	(3 left, 7 right)
17 June 1970	ovarian follicles	6.0 x 6.0 mm	(5 left, 3 right)
3 June 1969	ovarian follicles	9.0 x 9.0 mm	(6 left, 4 right)
7 June 1977	oviducal eggs	16.0 x 9.0 mm	(5 left, 5 right)
2 June 1965	oviducal eggs	20.0 x 7.0 mm	(4 left, 6 right)

For 11 clutches in seven different years, average date of oviposition was 1 July ± 1.8 days (ranging from 24 June to 11 July). One specific incubation record in 1978 was 53 days (from 25 June to 17–18 August). An unusually late clutch was indicated by eggs that were hatching on 10 October 1961.

Information on numbers of eggs per clutch was obtained from clutches in natural nests (four), from dissected females (five), and from 31 clutches deposited by gravid females temporarily held in the UKNHR laboratory. Clutches were obtained in 15 different years. Mean clutch size was 10.2 ± 0.47 eggs (5–16 eggs per clutch, number of clutches = 40). Clutches were rather evenly distributed throughout this wide range: seven clutches with 12 eggs, six with 10 eggs, six with nine eggs, five with seven eggs, four with eight eggs, three with 11 eggs, three with 15 eggs, three with 16 eggs, two with six eggs, and one with five eggs.

As in many other reptiles, size of clutch was influenced by size of female, and in many instances the smaller clutches were those of newly matured individuals (Fig. 4). However, other factors may have been even more important in determining clutch size, since the correlation between body size and egg number was not close. It must be said that in both natural nests and clutches laid in confinement, there was always the possiblity of missing eggs. Only a single egg could be found in one instance of a normally-appearing gravid female confined in a gallon jar of loose damp soil. She probably had eaten the other eggs in the clutch. In most years only small samples were available, but in 1966 there were 11 clutches (mean = 10.45 eggs, range of 5–16) and in 1969 there were nine clutches (mean = 10.67 eggs, range of 6–15 eggs per clutch). In each of these years the range of clutch size was comparable to that for all other years combined, and it seemed that the difference between years was relatively minor.

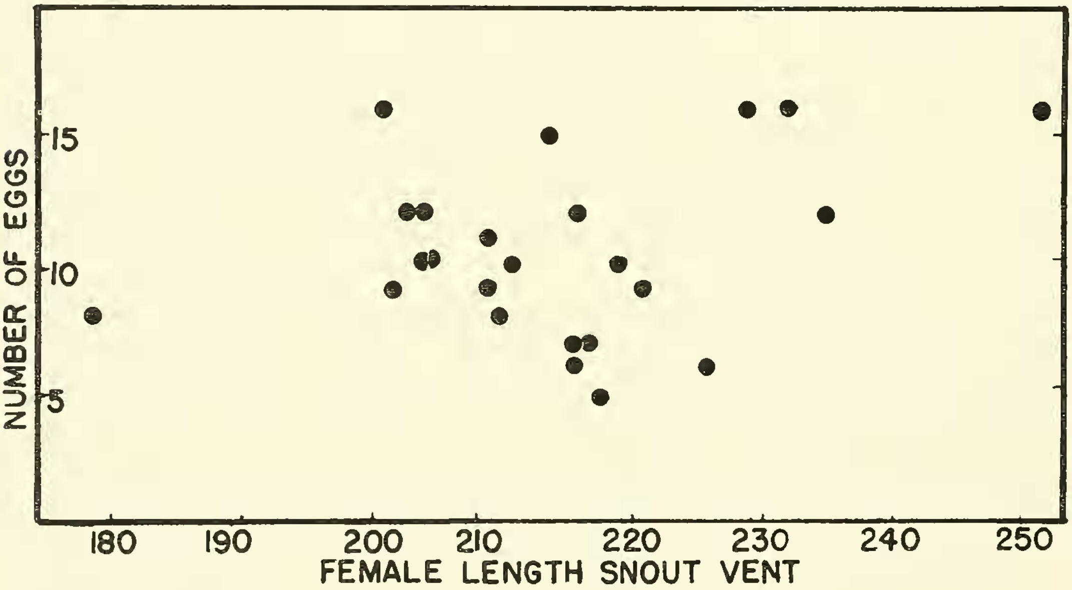

Fig. 4. Relationship of eggs per clutch to female snout-vent length in *Ophisaurus attenuatus*.

In most instances, confined females stayed beneath the surface in their containers and shaped a nest cavity by pressing against the soil around them and compacting it. Usually a female was found coiled around her clutch, but when the soil was too loose to be molded around a cavity, the eggs tended to be scattered. Checking on a clutch involved disturbance or destruction of the nest cavity and disruption of the female's brooding. Females showed no tendency to stay with the eggs or defend them when the nest cavity was opened, and they rarely returned to their clutches after such gross disturbance. It therefore became routine procedure to release the female after oviposition and allow the eggs to incubate without her. Individual eggs and some whole clutches succumbed to desiccation or fungi, but hatching success in general was high, suggesting that attendance by the female was not essential. In fact, it can only be speculated what useful role the attending female might have played because she did not raise the temperature of the eggs nor did she defend them against predators. Perhaps her movements caused the eggs to be less susceptible to mold than they otherwise would have been while lying for long periods with one area of shell in contact with the substrate. Also (or alternatively) the female may have prevented or delayed drying by releasing drops of moisture from her bladder.

In some capacity, an attending female must have markedly improved her eggs' prospects. One consequence, however, was lack of an opportunity for second or multiple clutches and, in late summer, after producing a clutch and guarding it for many weeks with little or no food, a female would become thin, even emaciated.

Noble and Mason (1938) kept two females of *Ophisaurus ventralis* and their egg clutches in the laboratory and compared their behavior with that of incubating females of *Eumeces fasciatus*. The female *Ophisaurus* "guarded" their eggs by coiling around them in the nest cavity, recognizing them by olfactory test, and retrieving them when they were scattered; however, the females were timid and would not defend their eggs against small vertebrates such as mice that were potential nest predators.

In southern Arkansas, Trauth (1984) found that female O. attenu*atus* as small as 150 mm (SVL) had developing follicles indicative of sexual maturity and presumably would produce offspring at an age of two years. Hence, at that latitude generation time is shorter than in northeastern Kansas. Several literature records of clutches are available for the southern part of the range: McConkey (1954), seven, eight, 11 eggs; Blair (1961) in Oklahoma, 11 eggs; Force (1930) in Oklahoma, 15 eggs; Mount (1975) in Alabama, five, 10 eggs; Trauth (1984) in Arkansas, an average of 12.1 eggs in seven clutches (7–16 eggs per clutch). The mean number of eggs for the combined 14 clutches above is 10.9 (5–16 eggs per clutch). Gloyd (1928) mentioned a clutch of eight eggs from Franklin County, Kansas.

In 20 instances, weights of the newly laid clutch and of the female just before and/or just after oviposition were available from UKNHR. Clutches averaged 15.03 (5.13–18.89) grams. Relative clutch mass averaged 24.62 ± 1.94 (11.9–44.7%). This mean was somewhat higher than in most lizards (22.4 ± 7.3% in 83 oviparous kinds; 22.6 ± 8.4% in 10 viviparous kinds, [Vitt and Price, 1982]). However, it was lower than the average figures for snakes, either oviparous (34.6 ± 8.7% in 52 samples) or viviparous (28.1 ± 8.2% in 54 samples) (Seigel and Fitch, 1984).

Growth. For 64 hatchlings of eight broods, mean SVL was 56.8 ± 0.30 mm (50–63 mm). Several hatchlings were at or near the maximum size of 63 mm, but the two smallest (50 and 51 mm) seemed to be the runts of their respective litters, and the next largest in still another litter was 53 mm. Juveniles captured were mostly larger, but were assumed to have begun their post-hatching growth at 56.8 mm SVL, and by establishing a probable hatching date, an early growth rate could be estimated. One clutch hatched in October; however, late August was the usual hatching time. For six other clutches, 21 August was the mean hatching date (range of 13–28 August). Since 1 July was calculated to be the mean date for oviposition, and incubation of 53 days was observed, 23 August was suggested as a typical date for hatching.

A total of 34 first-year young were captured during the fall (in September, October, November, and one on the last day of August) and they ranged from 64 to 80 mm SVL. Assuming that each was of mean size at hatching and hatched on or about 23 August, individual growth rates ranged from 0.15 to 1.01 mm per day, but averaged 0.57 mm, and the majority fell within the range of 0.4–0.65 mm. This rapid growth rate was characteristic of the early weeks of life. Samples of young captured in spring and fall showed the following mean sizes (SVL): early September, 69.6 ± 1.10 mm (*n* = 12); late September, 71.3 ± 1.18 mm (*n* = 11); May, 80.0 ± 3.77 mm (*n* = 7); early June, 89.0 ± 1.11 mm (*n* = 26); late June, 97.1 ± 1.16 mm (*n* = 47) (Table 1).

TABLE 1. Mean lengths of first-year and second-year young of *Ophisaurus attenuatus* (excluding recaptures) at different stages of the growing season.

Time	*n*	First-year Young	*n*	Second-year Young
Early Sept	12	69.6 ± 1.10 (65–75)	16	135.3 ± 2.01 (120–145)
Late Sept	11	71.3 ± 1.18 (70–75)	9	130.6 ± 3.27 (120–150)
May	7	80.0 ± 3.77 (70–100)	25	145.8 ± 5.84 (130–175)
Early Jun	26	89.0 ± 1.11 (80–100)	52	154.0 ± 1.27 (135–185)
Late Jun	47	97.1 ± 1.16 (80–115)	52	161.0 ± 1.57 (135–185)
Early Jul	49	109.3 ± 1.54 (70–135)	25	162.2 ± 2.16 (140–185)
Late Jul	73	120.1 ± 0.92 (105–135)	62	176.0 ± 1.56 (145–200)
Early Aug	42	126.4 ± 1.56 (105–140)	38	185.2 ± 5.43 (165–200)
Late Aug	33	125.3 ± 1.55 (105–140)	34	183.8 ± 2.85 (160-200)

Evidently growth was much slowed in the cool weather of autumn preceding hibernation and in the weeks of spring after emergence, but with the advent of warm weather, growth increased to a maximum rate and then tapered off rapidly as the animal increased in size (0.66 mm per day from June to July, 0.58 mm per day from July to August, 0.30 mm per day from August to September). Table 1 shows the progress of growth as revealed by size groups of young at different times during the growing season. Only records of first captures were used to trace growth through the first two years to avoid error due to stunting effects that handling and processing might have had. First-year young formed a discrete size group until early July; by then the largest individuals, those that experienced accelerated growth, nearly overtook retarded individuals of the previous year's cohort at an SVL slightly above 170 mm. Most second-year individuals could be separated from those in their first or third years; however, overlapping of annual cohorts became increasingly apparent and made it difficult to trace the course of growth. Beyond two years there was so much overlapping that age classes could not be discerned.

A second approach to the problem of growth was through the individual records of those young marked and recaptured. However, it was suspected that deleterious effects of handling and marking may have stunted these individuals, causing them to lag behind the average growth rate of others not subjected to such treatment. The possibility of stunting was tested as shown in Table 2 by comparing mean sizes in young captured for the first time and those captured one or more times previously. These figures indicated that the captured and marked young were stunted and were, on the average, about 10% shorter than individuals not thus handicapped. The figures further demonstrated that after two or more captures the animal was no more stunted than it would have been if captured only once. Apparently capture, handling, and measuring had no harmful effects, but the scale-clipping system used in marking involved trauma for the animal that set back its growth.

TABLE 2. Size groups in second-year *Ophisaurus attenuatus* comparing first-capture records with those previously captured and presumably stunted.

	Mean SVL Early June	*n*	Mean SVL Late June	*n*
First-capture records	154.0±1.27	52	161.0±1.57	52
Individuals recaptured once	138.2±2.07	31	140.0±3.04	11
Individuals recaptured twice	138.8±2.81	21	152.7±2.91	9
Individuals recaptured three or more times	138.7±3.15	12	147.5±3.46	9

Hatchlings of the slender glass lizard sometimes weighed less than 1 gram (mean = 1.23 ± 0.053 grams, *n* = 26) whereas some large adults weighed more than 100 grams. Figure 5 shows growth, as reflected by weight, in successive bimonthly samples during the first two years of life. Only first-capture records were used to avoid inclusion of records of individuals that might have been stunted from the effects of previous handling and marking. Average weight gains from one period to the next were relatively small in the fall and were perhaps depressed by the inclusion of newly hatched young in each successive sample and by cool weather slowing metabolism. Weight gain was found

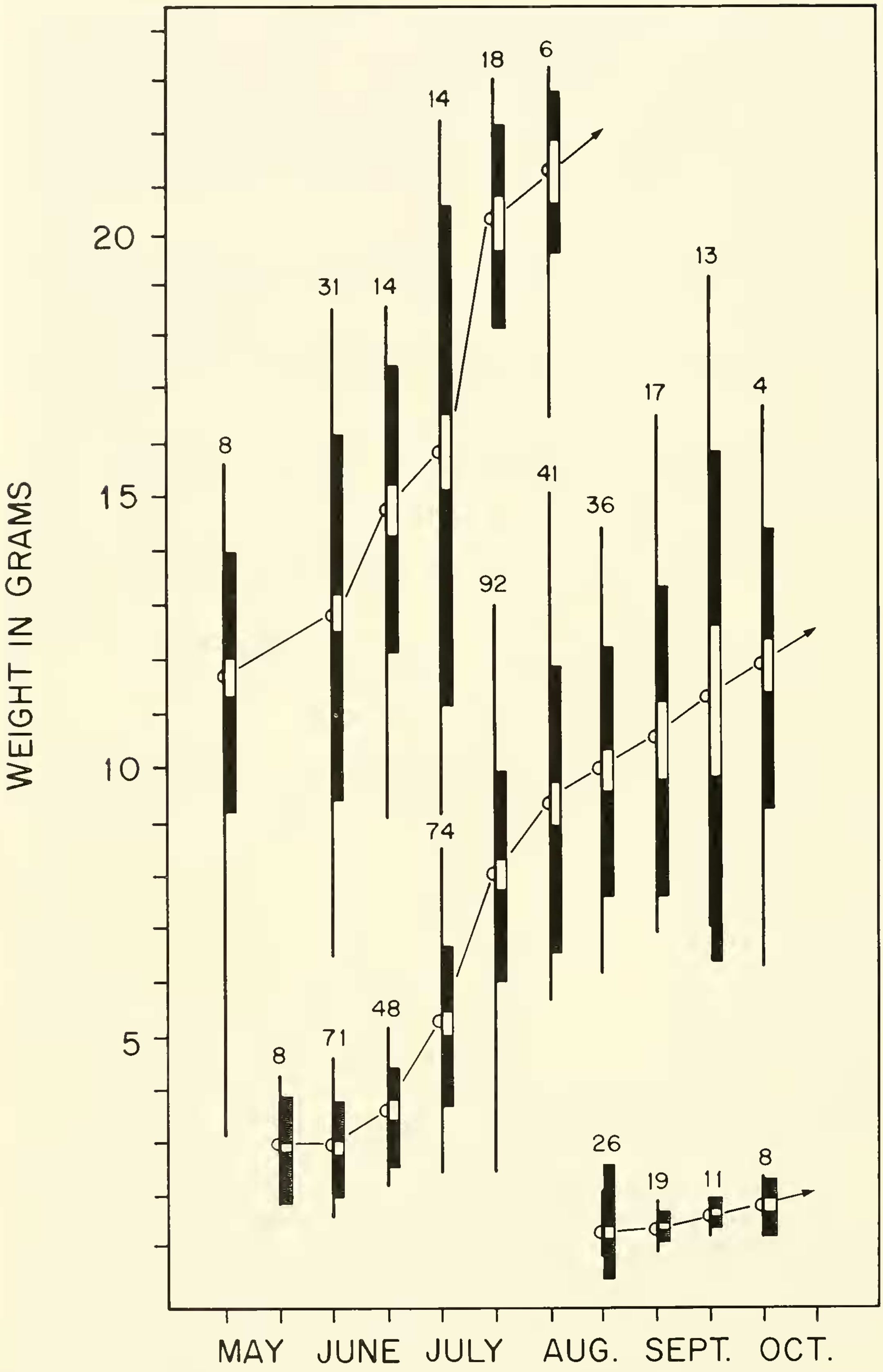

Fig. 5. Weights of glass lizards during their first two years; all records pertain to first captures. Mean, standard error, standard deviation, and range are shown for each sample. Number of lizards is at top of column.

to be most rapid in late June and early July and slowed during late summer and fall as the young completed their first year. Weight gain accelerated again in June and July of the second year. At hatching in late August, the largest young were more than twice the weight of the smallest. This disparity increased as growth proceeded, and by the following July, the largest young of an 11-month-old cohort weighed approximately six times as much as the smallest. Those young that were relatively small appeared to be normally healthy and vigorous, but selective mortality probably favored those that maintained an average or better growth rate. This latter group attained maturity sooner and had a better chance of laying more clutches and leaving more offspring over their lifetimes.

Beyond the age of two years, growth could be reconstructed only from the records of marked individuals, since discrete age groups were no longer recognizable. After an initial setback lasting up to two or three weeks, marked young recovered from their scale-clipping wounds and resumed normal growth. Table 3 summarizes growth in recaptured young. Those 150–159 mm SVL (a size normally attained by June of the second summer after hatching) were still growing rapidly and increased in length by more than 5 mm per month. By the time 180 mm was attained, growth was a little slower in females than in males, and this difference increased as the animals approached mature size. Growth projected beyond the age of two years (Table 4) was based on the records for recaptured individuals (with allowance for stunting in the weeks following marking).

TABLE 3. Gain in snout-vent length (SVL) per month in immature *Ophisaurus attenuatus* recaptured after periods of months (all lengths are SVL in mm). SC = size class at original capture; CM = combined months elapsed between captures; *n* = number of lizards sampled; MG = mean gain in length per month; CG = combined total length gained; RG = range of length gained in individuals; M = male; F = female.

SC	*n*	CM	MG	CG	RG
50–159	28	133.5 (2.0–14)	5.20 (2.50–12.80)	695	10–61
160–169	22	125.5 (1.5–20)	4.26 (2.00–12.50)	535	6–66
170–179	31	128.0 (1.5–20)	4.05 (1.25–14.60)	518	5–71
180–189:	18	105.0 (1.5–19)	4.25 (1.50–10.50)	446	6–63
M	9	56.0 (1.5–19)	4.54	254	8–63
F	9	49.0 (1.5–10)	3.92	192	6–42
190–199	4	31.5 (4.5–17)	2.98	94	4–43
M 200+	18	137.5	2.57	352	3–53
F 200+	3	24.0	1.79	43	5–26

Most adults that were recaptured after several months or several years had grown in the interval; however, the amount of growth was highly variable. The following applied to growth in adults: 1) it continued throughout life; 2) the rate gradually slowed with increasing age; 3) males grew faster than females of corresponding size or age; and 4) because of individual variability, the members of an annual age cohort spanned a wide size range, and individuals of any given size might have included members of several or many annual age classes.

TABLE 4. Age–size correlation in a local population of *Ophisaurus attenuatus* based on discrete size groups in young and on recaptures of marked adults.

	n	Mean SVL (mm)	Range (mm)
Hatchling	64	56.8±0.30	50–63
One-year-old	42	125.3±1.55	105–140
Two-year-old	37	183.8±2.85	165–200
Three-year-old			
Males	17	213.5	196–223
Females	6	206.0	201–216
Four-year-old			
Males	28	226.0	208–241
Females	27	221.0	203–242
Five-year-old			
Males	27	230.0	212–248
Females	11	224.0	212–243
Six-year-old			
Males	16	235.0	198–249
Females	2	232.0	218–246
Seven-year-old			
Males	11	246.0	236–265
Eight-year-old			
Males	8	248.0	235–262
Nine-year-old			
Male	1	254.0	251–259

Table 4 shows the correlation between age and size. Some of the older classes of six-, seven-, eight-, and nine-year-old lizards were already adolescents or small adults when first caught and marked, and each was assumed to be the age most typical for its size. For example, an SVL of 226 mm was the mean for four-year-old males, and individuals of this length or near it upon first capture were tentatively assigned to the four-year-old class even though some may have been retarded five- or six-year-old animals. Because of this possible source of error, and the fact that some samples were small, the means were probably inexact; those for three-, four-, and seven-year-old males seemed a little too high.

Spatial relationships. Slender glass lizards lived in individual areas or home ranges with which they were thoroughly familiar, but these areas did not appear to have any one focal point such as a "den" or "home base." The lizard's requirements for shelter were easily satisfied, and when it was inactive, it may have rested almost anywhere concealed beneath the surface mat of living and dead plant material. When forced to find deeper shelter for egg-laying, hibernation, or escaping heat and drought, the lizard may have utilized any of the abundant old tunnels left by burrowing mammals such as voles (*Microtus ochrogaster*) and moles (*Scalopus aquaticus*). On rare occasions in cool weather glass lizards were found beneath sheets of corrugated metal placed to attract such ectotherms, but, unlike some kinds of snakes, they did not regularly return to such a site.

Relatively few captures were made with traps; most slender glass lizards were captured when they were active on the ground surface. Only a few times were the animals caught at exactly the same place on successive occasions. Frequently the capture was at a separate but nearby location. The average distance between successive captures (n = 602) was 32.8 m (Table 5); also there were differences between different classes of individuals according to age and sex. For instance, adult male distances between successive captures were about 1.75 times the distance for first-year young, with adult females and

TABLE 5. Mean movements (distance in meters) between captures and estimated home ranges within a single season for *Ophisaurus attenuatus* of various age categories. 1st = first-year young; 2nd = second-year young; 3rd = third-year young; 4th = fourth-year young; AM = adult males; AF = adult females; CS = combined samples.

	1st	2nd	3rd	4th	AM	AF	CS
Total movements recorded	189	174	72	43	92	32	602
Range of movements	0–214	0–246	0–246	0–85	0–246	0–214	0–246
Mean movements	27.60	27.75	42.40	30.50	48.29	31.16	32.80
Number of long movements[1]	6	10	10	3	7	1	37
Mean, excluding long movements	22.8	21.3	27.57	26.50	37.30	25.20	27.00
Estimated home range (hectares)	0.16	0.14	0.24	0.22	0.44	0.20	0.23

[1] Considered to involve probable home range shifts.

partly grown young falling between these extremes. Doubtless various types of movement are included in these averages, including routine foraging and seasonal shifts.

Based on records of adult males only, distance between capture points increased with elapsed time, so that it was nearly four times as great after four seasons as in the first few days (Table 6). The implication is that home ranges were ephemeral and changed continually.

TABLE 6. Distances between successive capture points of individual adult male *Ophisaurus attenuatus*, arranged according to elapsed time.

Time span of records	Mean Distance (in meters)	Range (in meters)	*n*
1–5 days	25.0	0–70.5	14
6–15 days	53.9	18.3–116.0	15
16–150 days	58.7	3.0–248.0	62
2 seasons	62.9	0–288.0	46
3 seasons	92.0	4.6–232.0	12
4 seasons	95.6	36-128.5	3

Table 8 shows that for slender glass lizards of each age and sex class there were more distances between successive capture points of 5 to 10 m than in any comparable range, and the number tended to decrease gradually up to 100 m. Only a few movements between successive capture points were greater than 100 m. Home ranges were variable in size and shape and were larger in adults than in juveniles and larger in adult males than in adult females. The large number of distances between successive capture points that were less than 10 m suggested that some home ranges may have been in this order of magnitude, at least for the narrower dimension, and the scarcity and irregularity of distances between successive capture points exceeding 100 m suggested that these movements were beyond the limits of the regular home range. Excluding the few very long movements (those exceeding 100 m), the average distance between successive capture points for all animals was 27.0 m, and ranged from 21.3 m in young to 37.3 m in adult males. Because glass lizards had no focal point within the home range and seemed to move about at random, each pair of capture records should have been randomly situated with respect to each other, and their average distance should have been equivalent to half the diameter of the area used. The size of such an area was calculated from the formula, πr^2, and although the area was rarely a perfect circle, it might tend toward circular shape in homogeneous habitat. The home ranges in Table 5 were calculated on this basis and ranged from 0.14–0.16 hectares in the youngest cohorts of juveniles to 0.44 hectares in adult males.

Slender glass lizards were captured in five disjunct areas of habitat, including the bottomland field area of the UKNHR headquarters, where the great majority of captures were recorded, and four smaller upland areas to the northwest, north, and northeast, where there were fewer captures. In 21 instances, animals moved between upland and bottomland areas in shifts that must have involved abandonment of an original range and crossing of woodland strips where these lizards did not ordinarily occur. The woodland was deeply shaded in summer and lacked the type of ground vegetation normally preferred by the lizards. Causes for the shifts were not evident. However, in eight instances the animals that made the shifts were sexually mature females which were known to have been resident for periods of years on the original area before leaving it. In seven other instances, shifts were made by first-year males. Distances shifted averaged 490 m (266–784 m) in straight-line measurement, but doubtless the routes taken by the lizards were relatively circuitous.

Twenty slender glass lizards were equipped with radioactive wires of tantalum-182 and were trailed from day to day for varying lengths of time up to several months (Tables 7 and 8). These individuals yielded information not obtainable from the recapture of marked individuals including patterns of short-term movements, time of activity, and sites of nests and hibernacula. Seven animals trailed were adult males, five were adult females, seven were second- or third-year immatures, and one was a first-year juvenile. When found by trailing, these lizards were sometimes active above ground and sometimes inactive under shelter. In either case, disturbance of the animal was kept to a minimum so that its behavior would not be altered. However, when the radioactive signal remained in one spot over several successive checks, attempts were made to uncover the animal to ascertain that it was still present and had not dropped the tantalum wire.

The pattern of movements revealed by trailing was erratic. In foraging, a lizard moved slowly and stealthily with frequent long pauses. Movements were gradual with the cryptic color and pattern effective enough so the lizard was well protected from predators. In its daily foraging, a lizard normally confined its activities to an area within a few square meters. No permanent "home base" or shelter was utilized. Instead, a lizard that had finished its foraging wriggled under the surface litter of old dead vegetation, or into a burrow for concealment during its resting period. For several successive days, its resting spots may have been in the same direction and may have even been uniformly spaced; then it might have made an abrupt change in direction and distance covered.

The average day-to-day shift was 17.2 m ($n = 514$), and differed according to age and sex as follows: adult males, 20.9 m ($n = 207$); adult females 16.3 m ($n = 127$); immatures, 15.2 m ($n = 153$); first-year juveniles, 3.5 m ($n = 27$). These means were increased (except in the case of juveniles) by inclusion of occasional relatively long movements. Table 8 brings out further differences between these four groups. It shows that for males and second- and third-year immatures, shifts between 5 and 10 m were most frequent, but for adult females and especially for first-year juveniles, movements of less than 5 m were the most frequent.

TABLE 7. Movements and histories of individual specimens of *Ophisaurus attenuatus* marked with radioactive tantalum tags and trailed from day to day. SVL = snout-vent length in mm; Yr = year; DOT = dates of trailing; NTF = number of times found; NL = number of locations; DAU = dimensions of area used in meters; AC = area covered in hectares; U = unknown; M = male; F = female; Sub = subadult; Juv = juvenile; HG = halfgrown.

Age	Sex	SVL	Yr	DOT	NTF	NL	Days	DAU	AC
Adult	M	—	72	25 Apr–30 Aug	139	95	85	293x72	0.78 & 0.12
Adult	M	—	72	1–3 May	4	4	3	190x20	0.020
Adult	M	220	73	30 Jul–9 Aug	13	10	11	112x50	0.070
Adult	M	208	77	30 Apr–15 Jun	39	34	33	75x41	0.390
Adult	M	236	77	27 Jun–21 Jul	27	20	24	76x49	0.140
Adult	M	223	—	7 May–27 May[1]	2	2	2	12x00	0.000
Sub	M	194	—	7 May–25 May[1]	79	75	74	82x30	0.380
Adult	M	—	72	5 Apr–24 May	39	32	21	110x50	0.075
Adult	F	—	71	13 May–19 Sep	114	49	80	73x26	0.100
Adult	F	216	73	13 May–27 Jun	42	32	36	128x43	0.250
Adult	F	—	74	3 Jun–30 Aug	29	15	30	104x27	0.800
Adult	F	224	74	25 Apr–2 Jun	30	24	22	206x43	0.140
Adult	F	230	77	27 Jul–15 Aug	17	17	14	79x35	0.220
Adult	F	215	77	10 May–27 Jul	62	3	62	58x10	0.001
Juv	U	80	73	8 May–18 Jun	43	25	34	18x17	0.010
Juv	U	114	73	23 Aug–12 Oct	34	29	33	61x26	0.090
HG	U	—	74	2–16 May	7	7	7	46x3	0.010
HG	U	—	74	25–28 May	7	3	4	34x6	0.020
HG	F	169	78	22–24 Jun	9	8	3	14x9	0.010
Juv	U	—	77	13 Jul–18 Aug	33	26	31	61x20	0.080
HG	M	174	78	22–24 Jun	10	7	3	50x9	0.050
HG	U	—	74	23 May–3 Jul	8	8	8	61x9	0.030

[1] Date span shown is from May 1977 to May 1978.

Slender glass lizards that were in or near their hibernacula in fall and spring, and females associated with their egg clutches in nests in summer, often spent from several to many days at the same site without shifting. Other individuals also occasionally were found again at the same spot as when trailed previously, and presumably had not emerged. The reasons for such interruptions of activity were not evident, but it may be that the lizards had fed heavily and were digesting unusually large meals. Also, weather was probably involved in some instances. In 13.2% of the 667 trailing episodes that did not involve hibernacula or nests, the lizards were rediscovered in the same spot where they were found on the previous occasion; at 9.9% of their stopovers, the lizards remained, skipping one or more (up to six) periods of activity.

TABLE 8. Groupings of 514 day-to-day movements of Ophisaurus attenuatus according to distance, age, and sex of the lizard. M = adult males (% of 207 movements); F = adult females (% of 127 movements); I = second and third year immatures (% of 153 movements); J = first year juveniles (% of 27 movements); C = combined sample (% of 514 movements).

	Day-to-day movements (in meters)												
	1–5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60+
M	16.4	22.7	10.6	10.6	11.1	5.8	4.3	6.3	2.4	1.4	1.4	1.9	4.8
F	28.4	19.7	17.3	12.6	7.9	1.6	4.8	1.6	—	1.6	—	—	4.8
I	20.9	24.9	11.4	13.1	8.5	7.2	4.6	2.0	0.7	0.7	0.6	0.7	2.0
J	81.0	16.4	2.6	—	—	—	—	—	—	—	—	—	—
C	23.1	22.1	12.6	11.6	9.0	4.4	4.2	4.0	2.0	1.0	1.0	1.0	4.0

Temperature relationships. Slender glass lizards were found in the open most often at air temperatures between 23° and 28° C with a roughly normal distribution over this 5° range (Fig. 6). Body temperatures averaged some 3.6°C higher than ambient air temperatures and were concentrated in a 5° range (26°–31°C). During most of the season of activity, the daily activity cycle was found to be distinctly bimodal with peaks in the morning and late afternoon and little or no activity during the midday hours (Fig. 7). These activity cycles were based upon records obtained in June 1966 with Central Standard Time. Collecting effort was not, of course, uniformly distributed over the day, but was concentrated at the times that experience indicated were most productive. Small numbers of the lizards were captured between 1300 and 1700 hours only on occasional unseasonably cool or rainy days when the change in the weather stimulated bursts of activity at times when the lizards ordinarily would have been inactive under shelter.

Behavioral thermoregulation occurred as indicated by the fact that active slender glass lizards nearly always had body temperatures higher than adjacent air temperatures. The regulation of body temperature was complex; unless the animal was receiving radiant heat, its temperature was determined by a combination of the adjacent air and substrate temperatures and depended partly on the conductivity of the substrate and the relative amount of body surface contacting it. Glass lizards were seldom seen to bask in full sunshine.

In tall-grass habitat, with activity largely limited to the hours when the sun was low, the body was often screened by vegetation so that only a small part of it received sunshine. Much of the activity was near or after sunset, or on overcast or rainy days when basking was not possible. Compared with various teiids and iguanids which function efficiently at relatively high body temperatures and have a narrow range of preferred temperatures, glass lizards were normally active at considerably lower body temperatures and were active over a relatively wide range of temperatures.

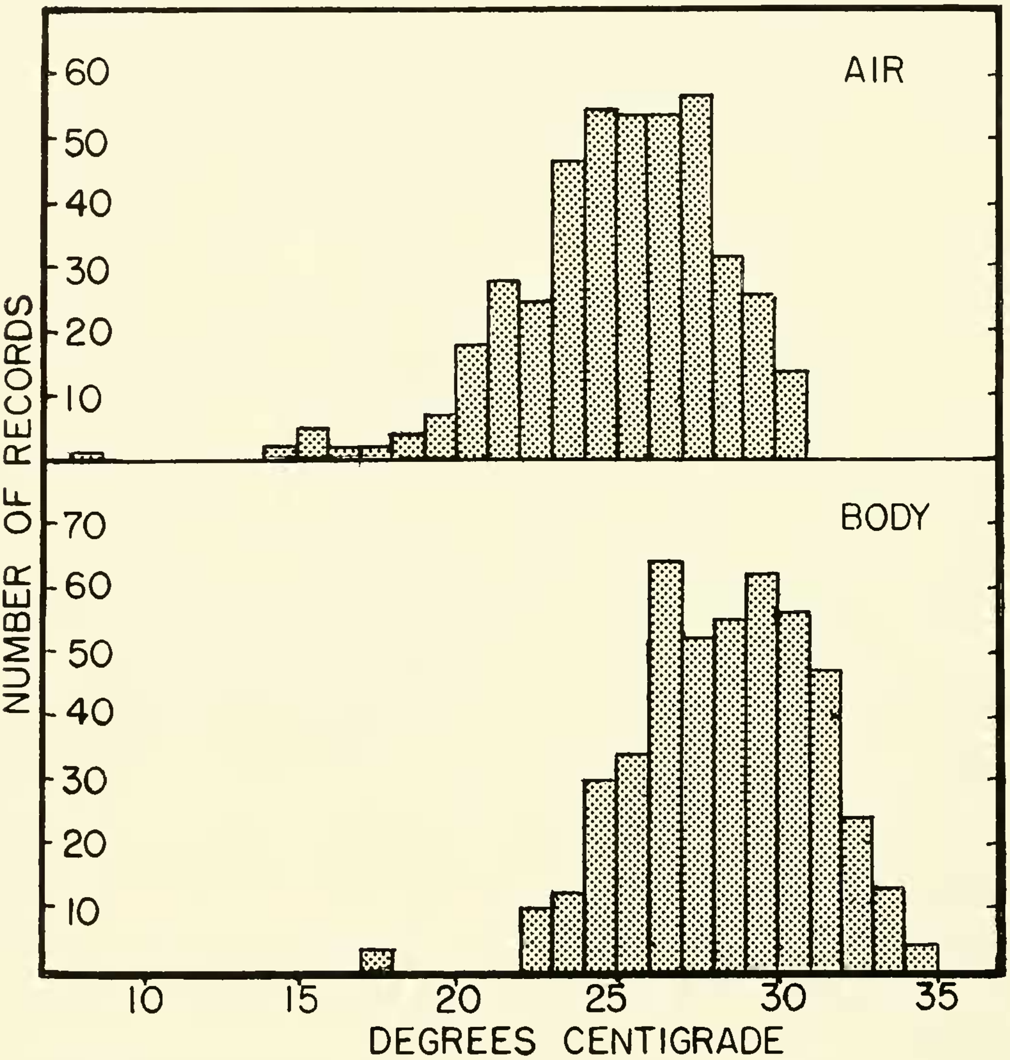

Fig. 6. Body (cloacal) temperatures taken with a Schultheis quick-reading thermometer, in glass lizards captured while active, and adjacent air temperatures for most of the same captures.

Active slender glass lizards at the moment of capture had body temperatures from 17.4° to 34.7°C, but most commonly, body temperatures were between 26° and 27°C and nearly as often between 29° and 30°C. Two individuals with body temperatures of 17.7°C each were captured at air temperature of only 8.4°C, at the beginning and end of the season of activity, 22 April and 4 November, respectively. In both instances, the animals had succeeded in raising their body temperature well above air temperature by

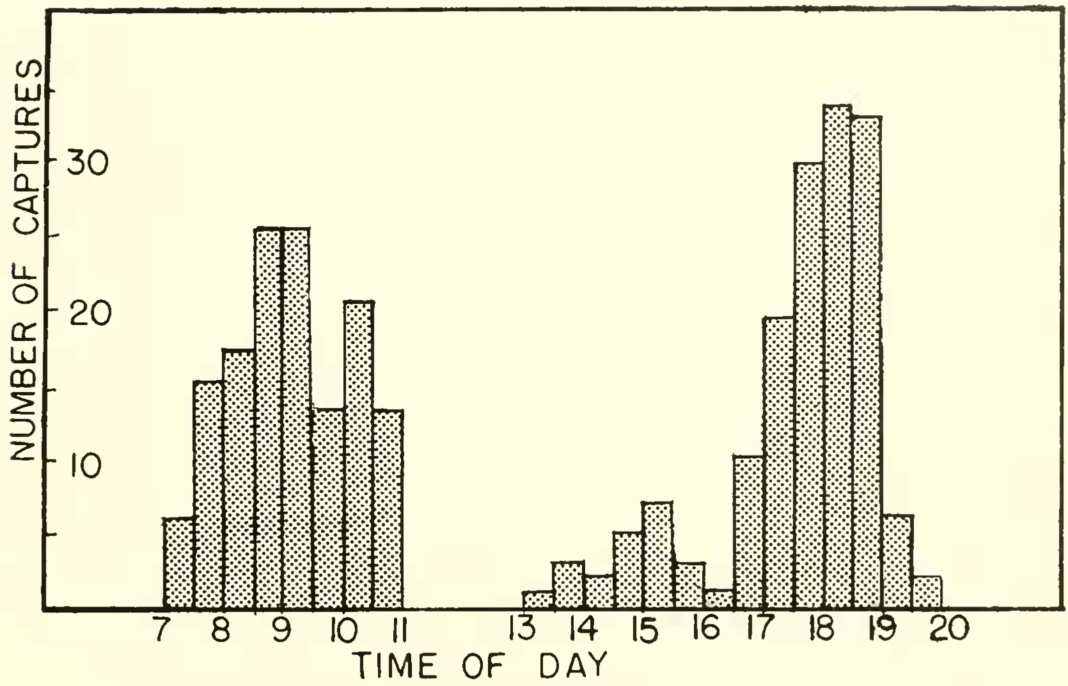

Fig. 7. Times (CST) of capture of glass lizards in June 1966.

basking, but their body temperatures were still much below the preferred range. The 22 April capture was made at 0930 hours.

Body temperatures in four groups of slender glass lizards (adult males, adult females, first-year young, and second-year young) suggested a possible tendency for slightly higher temperatures in adult males than in females or young (Fig. 8).

Hibernation. No slender glass lizards were found actually hibernating, but limited information on their location and associated behavior was obtained from individuals that were carrying radioactive tags. These lizards did not leave their summer range or undergo any sudden change in activity in autumn. However, with the onset of cool weather there was a gradual reduction in surface activity, and the lizards stayed underground in tunnels of voles (*Microtus ochrogaster*) and moles (*Scalopus aquaticus*) in observed instances. As temperatures declined, activity was decreased and lizards retreated to lower levels. A second-year juvenile that was trailed through late August and September was lost for several days in early October and its signal was located underground on 10 October. Two days later the lizard had moved about 3 m south and much deeper, apparently without emerging from the tunnel; it remained in this last site through the winter. An adult male remained in its hibernaculum until 22 April, but shifted 24 m on the day of its emergence.

On 5 April 1972 at 1450 hours and an air temperature of 22°C, an adult male was found to have left his deep hibernaculum and was just beneath the soil surface in a mole tunnel. Five minutes later he had emerged on the surface 1 m from the spot where he had been detected. During the afternoon he moved

24 m northwest. On 6 April he was checked five times between 0830 and 1830 hours, and each time had moved several meters on the surface where temperatures ranged between 16° and 29°C. On the night of 6 April cooler weather returned, and the lizard remained underground in his new location for two more weeks until springlike weather on 22 April again stimulated him to emerge. The retreat underground from 6 to 22 April constituted a resumption of hibernation, but in a relatively shallow site where a rise in air temperatures could trigger a prompt response.

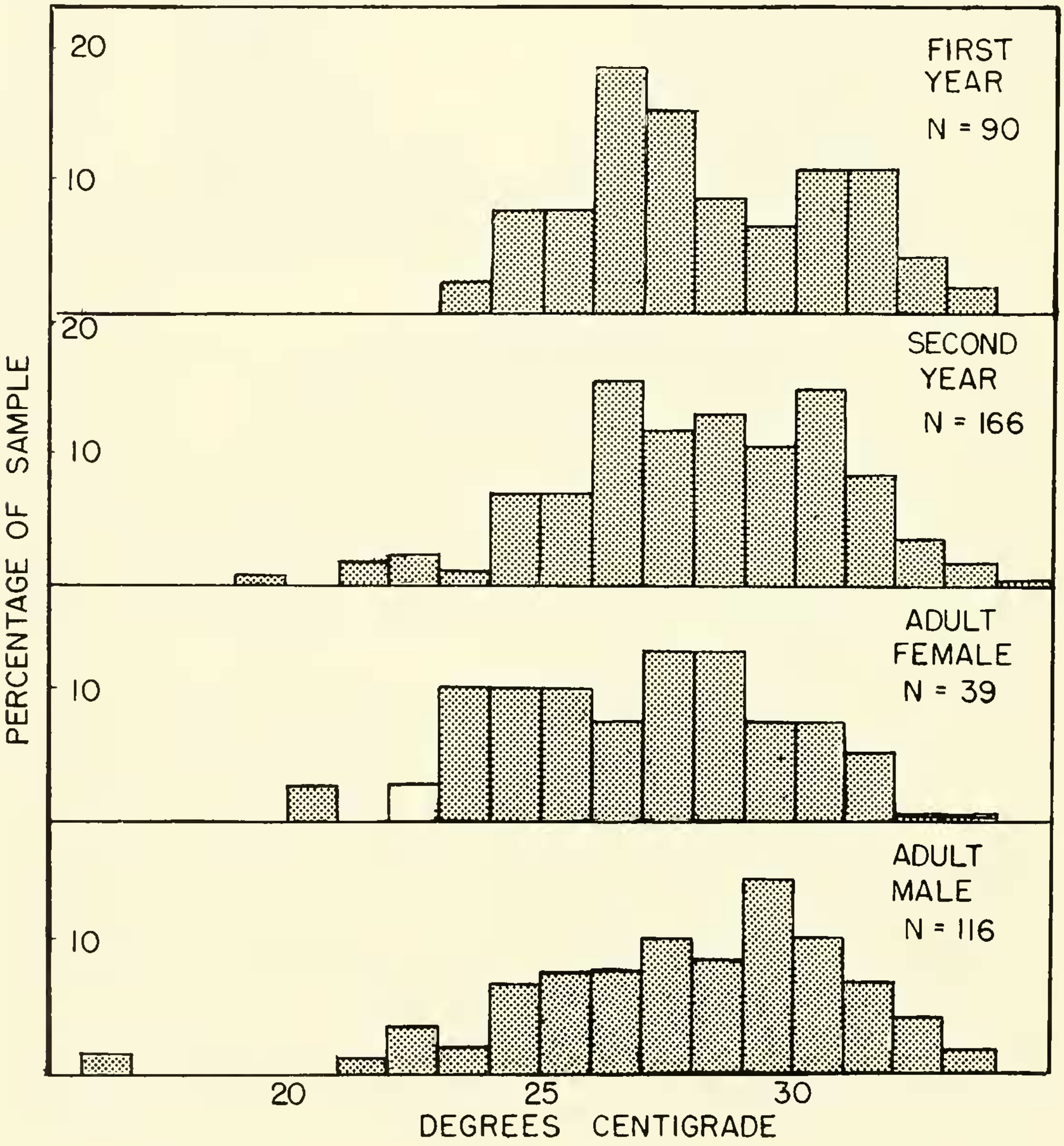

Fig. 8. Body temperatures compared in males and females, young and adults.

Unlike most local snakes which shared the same habitat but traveled to special hibernation sites in autumn, slender glass lizards remained and hibernated in the same area used during the summer. The chief requirements for a hibernation site were that it be below the frost line and that it provide some protection against small mammal predators, including moles, shrews, and mice, which might have attacked the hibernating lizard. Being unable to dig effectively, glass lizards were dependent on burrows of other animals for shelter but these burrows were mostly those of mammals that might have attacked them while they were hibernating. In having narrow, pointed heads and streamlined muscular bodies, these lizards were well suited to penetrate loose soil or debris that might accumulate in a long-abandoned tunnel. Slender glass lizards have the capacity to move backwards through tunnels by reversed wriggling movements guided by groping and tactile movements of the tail.

Food habits. The food habits of slender glass lizards are poorly known. Published statements of several authors pertain to the genus in general or else apply mainly to the European glass lizard or Scheltopusik (*Ophisaurus apodus*). It "eats snails and small rodents, crushing these with its powerful jaws" (Honders, 1975). It also "eats lizards, mice (which it crushes with one snap of its jaws), and other small vertebrates that abound in the rocky, broken country that it inhabits" (Schmidt and Inger, 1957). "Glass snakes feed by day on insects, especially grasshoppers. They sometimes take mice, fledgling birds, and the eggs of snakes and birds...said to eat snakes, including adders....The American glass snake...is said to eat earthworms as well as other underground animals" (Burton, 1975).

In keeping with its much smaller size, *O. attenuatus* takes smaller kinds of prey than does *O. apodus*, mostly invertebrates and especially orthopterans. In comparative tests of unfed neonate reptiles of 12 species, von Achen and Rakestraw (1984) offered individuals cotton swabs soaked in washings from favorite prey species (swabs with distilled water used as controls). The swabs offered to glass lizard hatchlings ($n = 14$, of two broods) had odors of prairie wolf spider (*Lycosa rabida*), cricket (*Acheta assimilis*), and grasshopper (*Melanoplus differentialis*). The swabs with prey odors elicited both tongue flicks and actual attacks in the *Ophisaurus* hatchlings which were more responsive than any of the 11 other species tested (including *Eumeces fasciatus* and local species of colubrine, natricine, and crotaline snakes). These findings emphasized the important role of Jacobson's Organ in the feeding of the glass lizard.

In the present study, a total of 508 food items were identified, 498 from the fecal droppings ("scats") of the slender glass lizards captured, and 10 others from stomachs of two lizards that were accidentally killed and from two individuals found in the act of eating prey. The scats averaged 2.1 items; 88 scats had only one identifiable item, 49 had two, 34 had three, 15 had four, nine had five, and two had six. In nine scats there was nothing recognizable. Some of these scats seemed to consist mainly of soil, and may have been residue from earthworms consumed, but predation on earthworms was not definitely confirmed.

Since the prey items found in scats were fragmentary, their biomass individually or collectively could not be determined. From the usual size of some of the favorite prey species, it was estimated that most commonly consumed prey was from 0.5% to 2% of the lizard's body weight, but occasional items were markedly larger or smaller than these limits. The occasional vertebrates eaten were relatively large meals, and 2.7% of the scats contained remains of a vertebrate. Of the 11 vertebrate prey items, four were small frogs (with tentative identification of *Rana blairi* and *Gastrophryne olivacea*) whose remains consisted of pelvic girdle fragments and patches of skin. There were four occurrences of small snakes, two of them identified as *Diadophis punctatus*. There were three occurrences of small mammals (all believed to be very young ones) including one identified from a tooth fragment as *Microtus ochrogaster*. Because they are much smaller, the young of *Reithrodontomys megalotis*, *Blarina hylophaga*, and *Cryptotis parva* are also probable prey.

The small chitinous fragments of arthropod prey were well mixed in each scat, often with the remains of several or many individuals in a single sample. Hence, identification to species often was not feasible, and there was often uncertainty as to the number of individual prey animals. Identified items included 23 unspecified "insects," 252 orthopterans (with 23 *Melanoplus bivittatus*, 18 *M. differentialis*, 10 *M. femur-rubrum*, 64 unspecified acridids, 25 *Arphia simplex*, 16 *Paratylotropidia brunneri*, two *Schistocerca obscura*, two *Syrbula admirabilis*, one *Daihinia brevipes*, 54 *Acheta assimilis* and/or other gryllids, 10 *Ceuthophilus maculatus*, six *Neoconocephalus robustus*, five *Amblycorypha rotundifolia*, and four *Orchelimum vulgare*), 85 coleopterans (including at least three scarabaeids and three carabids, in addition to one *Calosoma*), 17 caterpillars, two lepidopteran pupae, two cicadas, four ants, 57 spiders (including 12 *Phidippus audax*), and five snails (including two *Stenotrema leai*).

The common large salticid, *Phidippus audax*, was the only species of spider definitely identified in scats. Its iridescent green chelicerae were easily recognizable. However, two intact spiders, one in the jaws of a first-year glass lizard in July and the other in a stomach of one accidentally killed in June, were both penultimates of the large grassland wolf spider, *Lycosa rabida*. Because it was abundant in the glass lizard's habitat, was terrestrial, and was within the preferred size range, this may have been the species of spider most often eaten.

Table 9 shows some seasonal trends. Orthopterans, chiefly crickets, grasshoppers, and katydids, made up the greater part of the food at all times, but were least important early in the summer when most local species were in their nymphal stages and were very small. However, some insects that wintered as adults, notably the grasshopper *Arphia simplex*, were commonly eaten in spring and early summer. Caterpillars, beetles, snails, and spiders were prominent in the diet early in the activity season and were scarce or absent after midsummer.

Most of the prey animals taken were active types that probably could

TABLE 9. Seasonal trends in prey of *Ophisaurus attenuatus*. Percentages of monthly samples.

	n	%May	%Jun	%Jul	%Aug	%Sep	%Oct
Snails	9	0.8	2.9	—	2.2	—	—
Spiders	48	10.1	16.4	7.3	8.7	10.3	—
Misc. Insects	32	17.8	3.6	—	2.2	3.5	—
Caterpillars	20	8.5	3.6	1.8	—	10.3	—
Beetles	96	27.1	16.4	7.3	18.5	24.1	—
Misc. Orthopterans	69	8.5	27.8	29.1	3.3	3.5	11.1
Cave Crickets	12	—	5.0	7.3	—	7.0	11.1
Grasshoppers/Katydids	164	27.1	29.1	43.7	65.1	44.8	77.8
Combined Categories[1]	450	129	140	55	94	29	9

[1] Represents the number of food records for each month.

escape pursuit by a slender glass lizard. A sit-and-wait strategy, with ambush, must have been the normal method of hunting. Most often the prey was identified by movement and secured with a sudden lunge which was sometimes preceded by slow and stealthy approach. A small percentage of the animals taken, including pupae and snails, must have been detected by olfaction rather than vision. Occasional feeding on insects having repellent secretions, such as the large carabid beetle, *Calosoma*, was surprising. Most of the diet consisted of large, soft-bodied insects.

Predation. Many kinds of predators fed upon slender glass lizards regularly or occasionally in the area of this study. The opossum (*Didelphis virginiana*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), and bobcat (*Lynx rufus*) were all suspected predators but definite records were lacking. For the raccoon (*Procyon lotor*), Stains (1956) recorded one occurrence of *Ophisaurus* remains in 42 scats collected in spring from the Wakarusa River area about 10 km south of this study area. On many occasions raccoons were attracted to the wire funnel traps in which various small vertebrates, including glass lizards, were sometimes captured on UKNHR. These raccoons obtained their prey by bending back or wrenching off the end of the trap or by reaching through the funnel with one front paw, grasping and pulling out the trapped animal. Evidence of such theft was clear when the inward-directed wire prongs of the funnel had been bent back as the raccoon forcibly withdrew its paw, holding prey such as an insect, frog, mouse, or glass lizard. On several occasions, a detached tail remained in the trap to indicate that a glass lizard had been removed.

Because small reptiles were known to be preferred prey, skunks (*Mephitis mephitis*, *Spilogale putorius*) were believed to eat slender glass lizards and were observed hunting by olfactory and tactile search through the surface litter in places where these lizards stayed. Eastern moles (*Scalopus aquaticus*) and short-tailed shrews (*Blarina hylophaga*) may have occasionally preyed upon small glass lizards as indicated by the fact that the lizards often carried scars on the body or tail from wounds that must have been inflicted by small sharp-toothed predators. Both the shrew and the mole were common in the lizards' habitat, and the lizards often used old mole tunnels for shelter and escape. Attacks may have occurred at times when the lizards were partly or fully dormant underground and were unable to escape or defend themselves effectively. White-footed mice (*Peromyscus leucopus*) and harvest mice (*Reithrodontomys megalotis*) on several occasions killed or injured glass lizards caught with them in funnel traps. Both of these species of mice readily take animal food and could have attacked hibernating reptiles.

Remains of two slender glass lizards were found among 138 prey items brought to nests by broad-winged hawks (*Buteo platypterus*) on UKNHR (Fitch, 1974). The lizards were estimated to make up 1.4% of the prey biomass consumed by the hawks. There were 13 *Ophisaurus* occurrences in 1322 pellets of red-tailed hawks (*Buteo jamaicensis*) from many nests in eastern Kansas studied over a three-year period (Fitch and Bare, 1978).

Four of the 16 species of snakes on UKNHR were found to prey upon slender glass lizards. There were eight occurrences of glass lizards among 602 identified items in a food sample of the copperhead (*Agkistrodon contortrix*) (Fitch, 1960), and one occurrence each among 986 prey items of the yellowbelly racer (*Coluber constrictor*), among 56 prey items of the prairie kingsnake (*Lampropeltis calligaster*) (Fitch, 1982), and among 229 prey items of the ringneck snake (*Diadophis punctatus*) (Fitch, 1975). Taking into account the numbers of each kind of snake and the frequency of feeding, it was estimated that the biomass of *Ophisaurus* consumed annually would amount to 46 grams per hectare for the copperhead, 13 grams per hectare for the yellowbelly racer, and 3 grams per hectare for the prairie kingsnake.

Ringneck snakes in this area are known to feed almost entirely on earthworms; most kinds of vertebrates are too large to be swallowed by these small snakes. Only adult ringneck snakes are sufficiently large to swallow hatchling slender glass lizards. Since only one instance of such predation was observed, it was uncertain whether this was a rare aberration or whether the lizards comprised a small but constant percentage of the ringneck snake's food. The ringneck snake was so abundant (estimated at 1266 per hectare on a sample area; Fitch, 1982) that even occasional predation by it could have had drastic effects on the much less dense glass lizard population. It is tentatively suggested that the abundant ringneck snake constituted a major hazard to hatchling glass lizards and that a substantial proportion of lizards were eliminated before they grew large enough to be safe from such small predators.

Although quantitative data were not available to demonstrate the relative importance of various mortality factors, it seemed that at least a dozen kinds of predators, including snakes, hawks, and carnivorous mammals, fed upon slender glass lizards in the study area. However, none of these predators could be singled out as more effective than the others in the lizard's ecology. The lizard probably did not comprise more than a small percentage of the diet for any of these predators.

Caudal relationships. In hatchling slender glass lizards, body proportions differed from those of adults. The tail was relatively short and stubby in hatchlings, averaging only 182.5% of SVL. As allometric growth proceeded, relative tail length increased and attained a maximum of 206.6% (in males) when the lizards were between 140–150 mm SVL, a size reached most typically in May of the second spring after hatching. Relative tail length was slightly greater in males than females, not only in adults but also in young of all sizes in which the sexes could be distinguished. However, in those young of less than 100 mm SVL, sexing was difficult and uncertain. With increasing size beyond 150 mm SVL, relative tail length became progressively smaller, and in large adult males of 240–250 mm, the percentage had declined to 193.5% (Fig. 2).

Depending upon the size and sex of the lizard, an intact tail comprised about two-thirds of the total length, and its importance to the animal's survival and success could hardly be overestimated. One function was the storage of fat. By slightly increasing the diameter of the tail for its whole length the lizard could store a relatively large amount of fat without losing its streamlined contours. Also, the tail played an important part in the wriggling lateral movements by which the lizard progressed rapidly through dense vegetation. The importance of the intact tail to efficient locomotion was dramatically illustrated by incidents when an individual with a short tail, recently broken, or regenerated but stubby, was observed to be relatively slow in its escape speed compared with intact individuals, even though the lizards' movements were equally vigorous.

Another function of the tail was the distraction of predators; the tail might break as a lizard was captured, and its lively wriggling might gain the predator's attention for the moment required for the lizard to dart to safety. Because the tail occupied about two-thirds of the total length, the captured lizard was usually grasped by some part of its tail. A predator lunging at a moving glass lizard usually caught it well behind the middle and, if successful, grasped mostly the tail.

In view of the tail's importance in fat storage and locomotion, it seemed remarkable that besides shedding the tail in response to even slight physical trauma, a lizard might snap off its own tail when it was not even being touched, in response to excitement or danger. Our capture technique involved lunging and pinning down the front end of the animal while avoiding contact with the tail. Nevertheless, tails occasionally broke at the moment of capture. Much more often the newly captured lizard snapped off its tail after it was deposited in a cloth bag, and this was much more frequent if two were bagged together. On occasion, recaptured glass lizards that were already marked and were handled only briefly for weighing and measuring, were observed to snap off their tails as soon as they were released. The actual tail shedding was accomplished by a sudden lashing movement.

Figure 9 shows the percentages of intact tails in slender glass lizards of different size classes. In hatchlings, all tails were intact, but as larger size was attained, increasing numbers had broken and regenerated tails. In the three size classes of the largest adults, there were no intact tails, as all had been regenerated at least once. The histogram does not show a smooth regression as might be expected; in several instances there was a size class with a higher incidence of damaged tails than found in the next largest class. Sampling error was one possibility that might have accounted for this discrepancy; however, in the 70–80 mm SVL class there were nearly three times as many damaged tails as in the 80–90 mm class. It was quite possible that the data reflected the true situation, and that the small juveniles were especially subject to attack by abundant small predators such as the ringneck snake (*Diadophis punctatus*). Perhaps the early handicap of a broken tail was so damaging to the lizards' chances of survival that few of those that lost their tails lived long enough to be represented in the next largest size class.

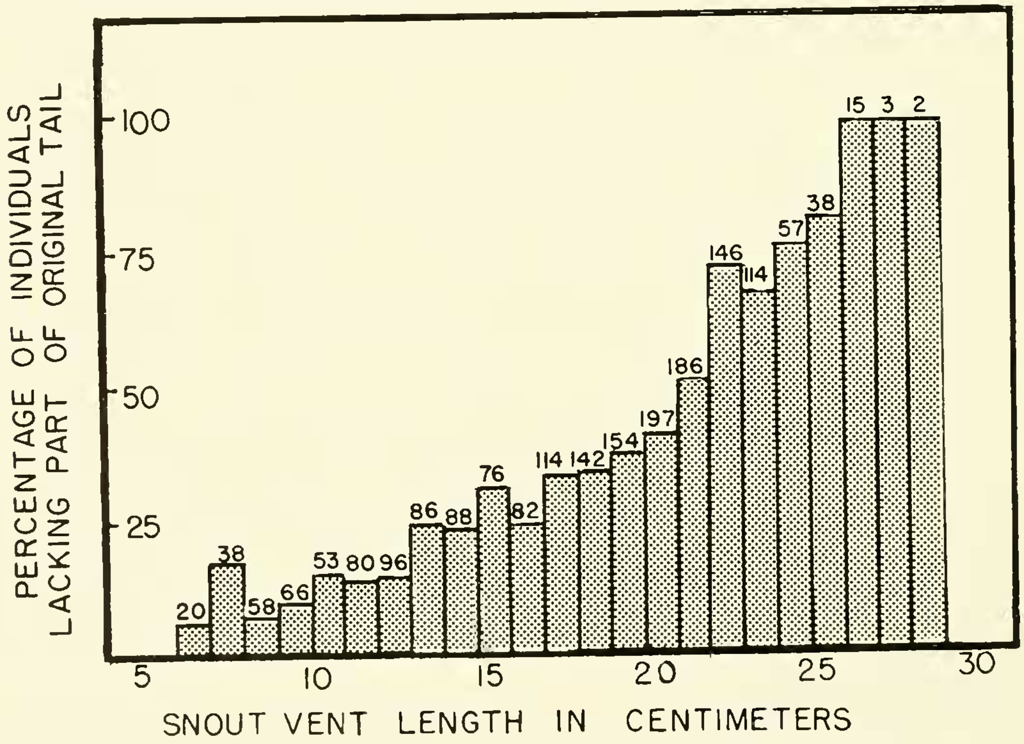

Fig. 9. Incidence of damaged tails, with part missing, in slender glass lizards of different sizes. Sample size shown by figure over bar.

Typical tail vertebrae of *Ophisaurus* are long and slender and each has a transverse fracture plane across its middle. When a break had occurred, the distal half of the vertebra involved was lost with the shed tail, while the proximal half remained on the tail stub. Externally the tail consisted of successive whorls of elongate scales, but there were two whorls to a vertebra and a break could occur only after every second whorl. In a regenerated tail there were no vertebrae and the tough, fibrous tissue was not subject to breakage. The regenerated tail was innervated from the spinal cord in the most posterior remaining vertebra of the original tail. Lacking any part of the central nervous system, the regenerated tail would have been inert and would have lost its anti-predator value if it were cut or bitten off out beyond the end of the original part. Regenerated tails, therefore, nearly always broke proximally from the point of juncture with the old tail, and with each successive break the original tail stub became shorter.

In the 209 instances in which freshly-broken tails were weighed, the lost piece ranged from less than 1% to more than 46% of the animal's total weight, with a mean of 12.9%. Loss of the tail thus could involve a sacrifice of nearly half the lizard's living tissues, and usually involved a substantial proportion. To the loss of blood, fat, and bony tissue, must be added the trauma of injury and serious handicapping in locomotion. Compensatory gains must have been great to justify this major sacrifice. Probably each tail loss marked an encounter with a natural enemy (hawk, owl, snake, opossum, skunk, or fox) and represented a crisis in which the lizard's life may have been saved by the effectiveness of its detached tail as a decoy.

Regenerated tails were always shorter than original tails, had less regular scalation, and were more abruptly tapered. The point of juncture between old and new parts could be easily discerned. At first the broken end was covered with a scab of dried blood, and no regeneration was noticeable for the first two weeks. The course of regeneration was erratic and unpredictable, with great inter-individual differences that could not be readily accounted for on the basis of size, sex, season, or location of the tail break. Most rapid growth occurred in the period of weeks after the break. After three months the regenerated tail might have been as much as 10% of the missing piece, or a little more. Growth subsequently tapered off. After the first year, growth had either stopped or had become extremely slow. The regenerated tail might grow to as much as 30% of the length of the missing piece but regeneration was usually less (Table 10).

From the instant of fracture, the detached tail wriggled with such lively and jerky movements that it was seen as a blur. The effect was especially confusing when the tail flopped about in dense vegetation. The movement consisted of a series of lateral contractions with left and right sides alternating. The broken end and the tail tip swung toward each other as the tail was bending; then the tail straightened and bent to the other side. The vigor of the movement depended upon temperature, and maximum activity occurred only at high body temperature at or near the lizard's preferendum. Both the amplitude and speed of the contractions decreased progressively over a period of minutes after a break. At the start there were about three contractions per second, but after eight to ten minutes there was barely perceptible

TABLE 10. Growth of regenerated tails, expressd as percentage of length of missing (original) tail in recaptured *Ophisaurus attenuatus*.

Elapsed time (days)	Length of regenerated tail as % of missing tail Mean	Range	*n*
0–15	0	—	19
16–30	1.29±0.36	0.00–3.30	12
31–45	6.59±1.31	3.40–15.1	11
46–60	6.73±0.88	3.90–10.3	7
61–75	5.69±0.82	1.50–7.30	7
76–90	11.40	11.00–12.10	3
91–105	8.98±1.41	3.90–12.5	5
106–120	9.25	6.00–14.2	4
12–13 months[1]	13.4	11.8–15.5	5
22–56 months[1]	15.3	8.20–30.6	13

[1] Including winter dormacy period(s) that amount(s) to more than half of each annual cycle.

movement. A touch momentarily stimulated the tail to renewed activity, and a pinch or prick elicited stronger response. A broken tail that had performed its course of contractions and had become inert could be induced by stimulation to perform several more twitches; the action could be repeated several times, but each time with a feebler response.

Figures 10 and 11 show the declining rate of contractions in broken tails in five specific instances. In each case, there was a lag of from 5–15 seconds from the time of the break until the count was begun. Variation in this lag time was, in part, responsible for the different shaped curves in the graph, because the rate of contraction was by far the most rapid during the first few seconds. Not shown was the trend toward rapid decline in vigor of movements. Contractions which at first were violent enough to flip the tail a distance of several cm finally subsided after four or five minutes to become barely perceptible twitches.

Parasitism. Loomis (1956) listed *Ophisaurus attenuatus* among the hosts of the common pest chigger, *Trombicula alfreddugési*, but actually the lizard seemed to have a high degree of immunity from this parasitic mite which, in its larval stage, attacks a great variety of vertebrate hosts. Only one chigger was found attached, and it was dead and dried on the lateral fold of a lizard. Loomis stated that the large, rectangular, closely-juxtaposed scales do not afford access to soft areas suitable for chigger attachment, and even the lateral fold is usually protected by the overlapping scale edges. Besides the single glass lizard carrying a dead chigger, 14 others taken during the season of larval activity (from areas known to be infested) were found to be chigger-free. On three occasions Loomis experimentally placed caged glass lizards in chigger-

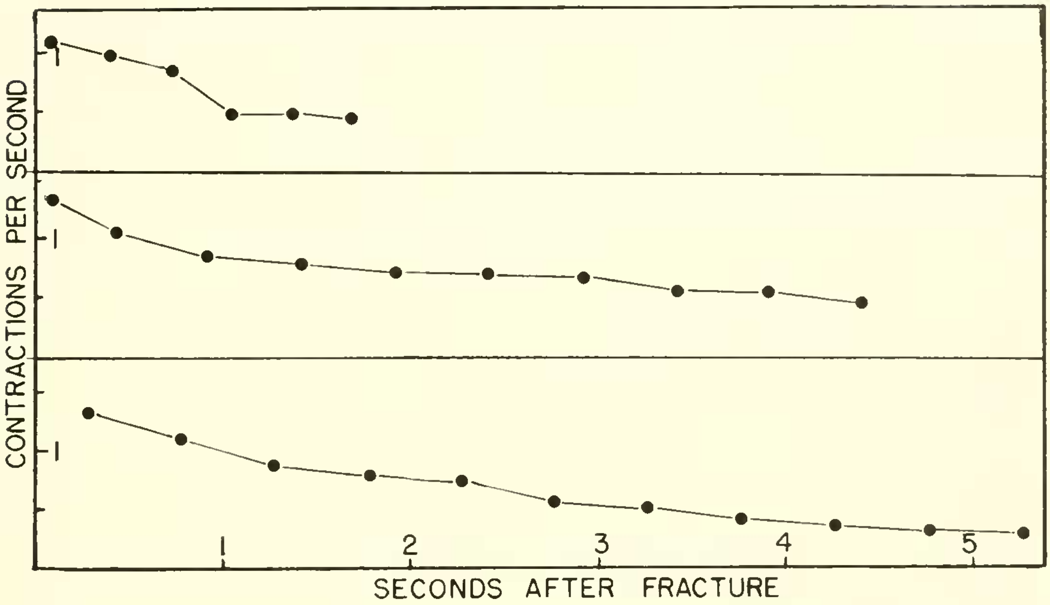

Fig. 10. Declining rate of contractions in three glass lizard tails after fracture.

infested spots and subsequently examined them for chiggers, but none had attached even though they had been seen crawling over the lizards.

This study did not include dissections to search for endoparasites, but one type frequently noticed was a tapeworm whose proglottids were often seen in feces voided by the lizards after capture. The proglottids were flattened, whitish, semitransparent, and about 8 mm in length. They were found mainly in adult lizards, but on 5 July 1966 three were voided by a newly captured first-year glass lizard (114 mm SVL). No ill effects were noticed in the lizard hosts. The intermediate host was not identified, but probably was one of the lizard's favorite prey species, perhaps a grasshopper, cricket, or katydid.

Numbers. Population density differed greatly among areas where slender glass lizards occurred; on each area there was seasonal change and also progressive change in numbers over periods of years. It was not feasible to catch all individuals on any area for a complete count. Hatchlings, appearing in August and September, were especially difficult to find. Young began to be well represented in samples in June and July after having approximately doubled their original length. Census figures based on mark-recapture ratios were somewhat distorted by seasonal changes. For instance, early in the season, first-year young still near hatchling size were inconspicuous, easily overlooked, and poorly represented, but adult males active in sexual search made up a disproportionately large percentage of the sample, especially in trap records. By midsummer, females tended to stay underground guarding their nests and were poorly represented in the records. The best data for estimating numbers were gathered from a 7-hectare block of pastureland, House Field-Horse Field- Picnic Field, that was largely isolated from other areas of favorable habitat. It was almost enclosed by woodland, with one end bordering a county road with cultivated land lying beyond. Because of this

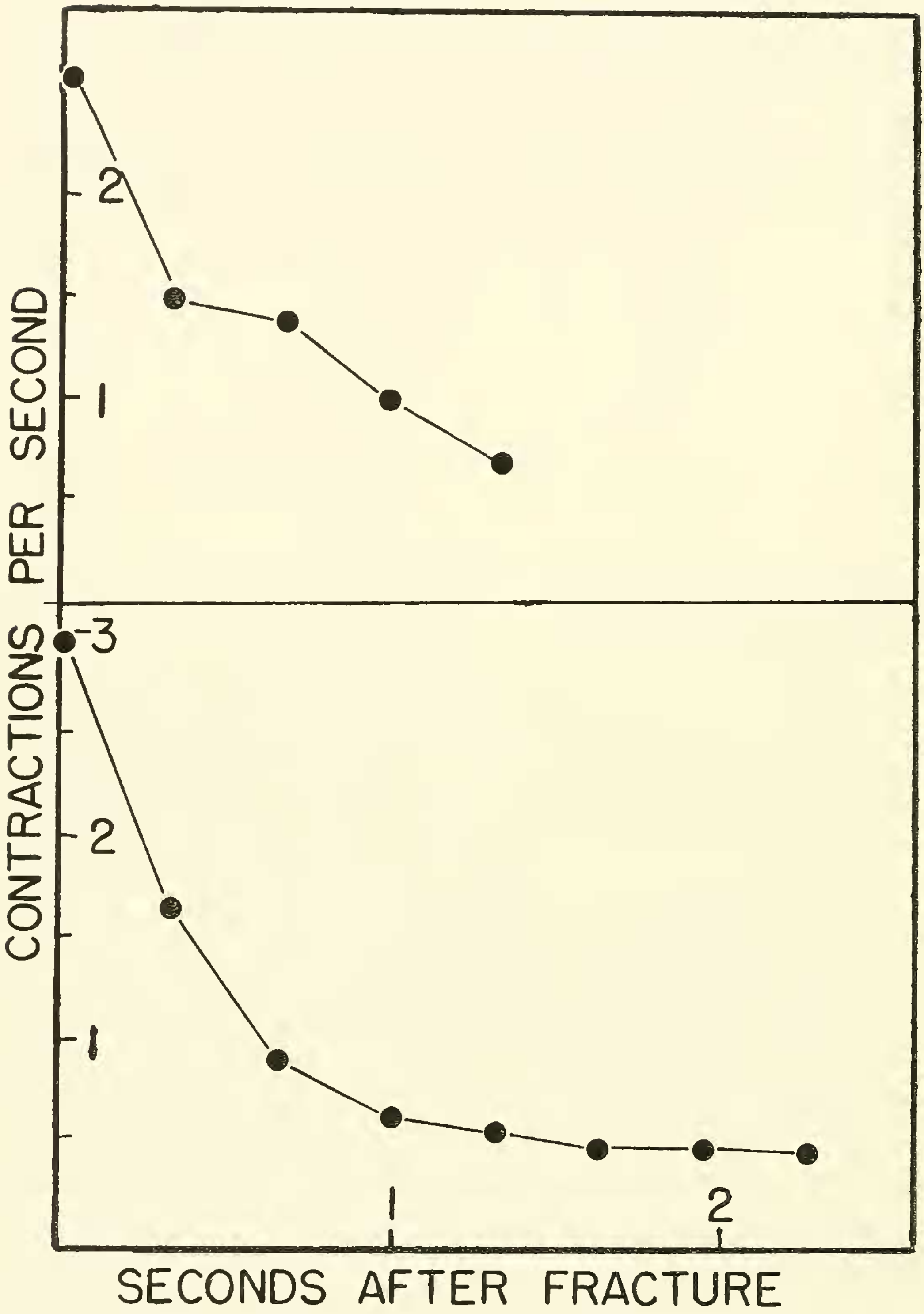

Fig. 11. Declining rate of contractions during first two seconds in broken tails of glass lizards in which counts were begun promptly after fracture.

isolation, there was hardly any emigration or immigration, hence, one of the conditions necessary for a mark-recapture census was met. Also, population increase by reproduction, as a source of error, could be ruled out because all young hatch at approximately the same time, and are recognizable as a distinct size group and were therefore excluded from the census calculations.

Census figures for the study area are shown in Table 11; there were six census periods each for 1965 and 1966, and two for 1967. Most of the figures were based upon month-long sampling periods. A group of individuals captured in one month and their ratio to others determined in the second month was used as a basis for the estimates. The population increased by reproduction in August and September and decreased through the remainder of the year. Hatchlings were not included in the August-September-October census figures. A consistent downward trend from May through October each year could have been expected in the censuses. However, they did not show such a trend, but instead fluctuated widely as the result of distorting factors. Variation from month to month in the kind and amount of effort devoted to obtaining samples, and the improving "catchability" of first-year young as their size increased, were factors which must have contributed to distortion of the figures. Those calculations based on only one to three recaptures were liable to deviate with a wide range of error. If such unreliable calculations based on few recaptures were excluded, there remained three estimates for 1965 (5–74 recaptures), averaging 519 animals; five estimates for 1966 (based on 11–74 recaptures), averaging 456 animals; and two estimates for 1967 (based on 9–12 recaptures), averaging 712 animals. These figures seemed fairly plausible in view of the total numbers captured in each annual sample: 232 in 1965, 332 in 1966, and 219 in 1967, the latter year with considerably less collecting effort than in the two preceding years.

With the same set of records, calculations were also made using the Jolly method of capture-recapture census, based on consecutive series of samples and the idea that individuals missed in one sample, but found in both an earlier and later one, revealed the relative chances of capture or non-capture. In every instance the Jolly census yielded a value much below that of the unrefined capture-recapture ratio, and in six of the seven Jolly censuses, the value was much below the actual number captured, showing the Jolly value to be erroneous.

The years 1965, 1966, and 1967 were used for the capture-recapture censuses in Table 11 because records were obtained in far greater numbers compared with other years, and substantial monthly samples were available. In other years, samples were too meager for month-to-month comparisons, but for several years capture-recapture censuses were made by dividing the season into an early sampling period of May–June and a late period of July–August–September–October (Table 12). In sequences of both the total annual catch and the capture-recapture censuses, a trend of gradual increase through the 1950s and 1960s followed by decrease in the 1970s and 1980s was shown. However, some deviations from this overall trend resulted from year-to-year variation in the amount of field work. For example, in 1968 I spent relatively little time on UKNHR and only nine slender glass lizards were captured in that year although they were still abundant.

Biomass estimates were made by assuming that the population had the

TABLE 11. Census figures for the 7 hectare study area of House Field and vicinity, comparing numbers of *Ophisaurus attenuatus* actually captured with figures from capture-recapture ratios.

Capture-recapture censuses and ratios	1965	1966	1967
May from June			
Census estimate	193	454	—
May captures	34	27	—
June captures	17	185	—
May–June captures	3	11	—
June from July			
Census estimate	569	505	645
June captures	17	185	181
July captures	167	112	32
June–July recaptures	5	41	9
July from August			
Census estimate	334	448	—
July captures	167	112	—
August captures	38	64	—
July–August recaptures	19	16	—
August from September			
Census estimate	608	327	—
August captures	38	64	—
September captures	16	51	—
August–September recaptures	1	10	—
September from October			
Census estimate	128	510	—
September captures	16	51	—
October captures	8	10	—
September–October recaptures	1	1	—
May–June from Jul–Aug–Sep–Oct			
Census estimate	635	545	780
May–June captures	209	209	199
Jul–Aug-Sep-Oct captures	193	193	47
May–June and Jul-Aug–Sep–Oct recaptures	74	74	12
Total number caught	232	332	219

composition shown in Table 13 and by using the following mean weights for different classes of individuals: large adults, 72.3 grams; medium adults, 60.0 grams; small adults, 49.0 grams; adolescents, 40.4 grams; two-year olds, 30.4 grams; one-year olds, 11.1 grams. Biomass was calculated as 2.15 kg per hectare in 1965, 1.93 kg per hectare in 1960, and 3.01 kg per hectare in 1967 from the population figures 519, 456, and 712, respectively. These figures excluded hatchlings, and represented the annual low point in numbers and

TABLE 12. Numbers of *Ophisaurus attenuatus* recorded over 37 years of field study on UKNHR.

		House Field Vicinity/7-hectare Study Area	
Year	Total Number captured	Number captured	Capture-recapture census[1]
1955	23	14	50
1956	49	56	96
1957	66	61	129
1958	72	47	496
1963-64	122	61	96
1965	354	232	635
1966	507	332	545
1967	344	219	780
1969	67	49	510
1970	44	31	150
1977-78	86	36	128
1984	30	10	25

[1] In years when samples were inadequate for capture-recapture census, numbers actually captured were as follows: 1949, 1; 1950, 6; 1951, 15; 1952, 13; 1953, 9; 1954, 20; 1959, 89; 1960, 71; 1961, 54; 1962, 36; 1968, 9; 1971, 29; 1972, 63; 1973, 40; 1974, 44; 1975, 12; 1976, 8; 1979, 33; 1980, 51; 1981, 17; 1982, 36; 1983, 22; 1985, 25; 1986, 23.

biomass just before the young of the year made their appearance.

Composition of the population and individual longevity. Most seasonal and annual samples that were obtained from the local population were believed to be somewhat biased because adult males and females had behavioral differences that would cause them to be unequally represented. Likewise, adults and young differed in behavior. In some years when relatively little effort was devoted to searching for glass lizards and catching them by hand, the catch consisted mostly of those obtained in wire funnel traps set for snakes. Young up to the mean one-year-old size were not caught in the traps because they were small enough to pass through the quarter-inch wire mesh. In May when adult males were active in sexual search, they made up most of the catch in the funnel traps. Reproductive females spent several weeks in summer guarding their egg clutches in underground nests, and during that time were not represented in the catch.

Samples were least biased in late summer and autumn when reproductive activities were over. A sample of 348 individuals was obtained for August, September, and October in the combined years of 1965, 1966, and 1967 (Table 13). This group was considered the best basis for showing composition of the population. Only 10 of the 348 were hatchlings, although this group

TABLE 13. Sex and age–size groups of 338 *Ophisaurus attenuatus* (excluding hatchlings) in August, September, and October of 1965, 1966, and 1967.

Size–Age Class	*n*		Size (mm SVL) Mean	Range	% of Sample
Large adults	10	(6 males)	255.5	248–264	3.0
		(4 females)	235.3	231–244	
Medium adults	41	(22 males)	233	220–241	12.1
		(19 females)	222.9	215–229	
Small adults	37	(14 males)	212.6	207–219	10.9
		(29 females)	208.25	202–209	
Adolescents (3-year-old young)	31	(15 males)	197.1	191–206	9.2
		(16 females)	197.0	195–199	
Two-year-old young	71			151–193	21.0
One-year-old young	148			97–147	43.8

should have outnumbered both adults and partly grown immatures, if represented in its true numbers. Evidently hatchlings were so small and inconspicuous that they were generally overlooked as they hid beneath the tall grass or as they crawled through it without causing any noticeable movement of the stems.

One-year-old young were more than twice as numerous as two-year-olds in the sample, and likewise, two-year-olds were more than twice as numerous as presumed three-year-old adolescents. Hence, it seemed that there was 50–60% annual loss in a cohort of young after the first year. Considerably higher mortality could have been expected in the first year, because the hatchlings were vulnerable to relatively small predators such as the ringneck snake.

The ratio of 57 adult and adolescent males to 68 females suggested either parity or a slight surplus of females. Sex could not be determined in immatures except by dissection, and, therefore, was not known in the one- and two-year-olds of the sample. If half of the 68 adult and adolescent females produced an average of 10.2 eggs each on a biennial cycle, their combined annual production would have totalled 347 eggs. During embryonic development and their first year after hatching, this cohort would have had to undergo 57.4% reduction to match the cohort of 148 one-year-olds in the sample. The schedule of attrition from the available data is shown in Table 14.

Many other species of lizards reach maturity within their first year of life and therefore have a more rapid population turnover than the slender glass lizard. This lizard was relatively slow in maturing with a low reproductive

TABLE 14. Survivorship in a hypothetical cohort of 347 eggs of *Ophisaurus attenuatus* estimated as the annual natural increase in a stable population of 348 lizards, including 68 adult females, half of which are fecund.

Year	Survivors from cohort of 347 eggs	Stage	% surviving through next year
First	347	eggs	42.6
Second	148	young	50.0
Third	74	young	60.0
Fourth	44	adolescents	60.0
Fifth	27	adults	60.0
Sixth	16	adults	60.0
Seventh	10	adults	60.0
Eighth	6	adults	60.0
Ninth	4	adults	60.0
Tenth	2	adults	60.0

potential. However, most individuals did not survive for many seasons. The majority of the 1237 recaptures were recorded in the same year that the lizard was first caught and marked. Table 15 shows the trend of rapidly dwindling numbers with passing years; only one of 2067 survived over the maximum span of nine years. Two others survived over eight seasons, four over seven years and ten over six years. These 17 individuals with the longest life spans were missed in 45% of the years that they were known to be present. Five consecutive years of records were the maximum, represented by just one lizard; there were two lizards with four consecutive capture years and 34 with three consecutive capture years.

TABLE 15. Distribution by years of records of 2116 marked *Ophisaurus attenuatus* recaptured. S = span of individual records; C = consecutive years of individual records.

Number of years		1	2	3	4	5	6	7	8	9
S	*n*	1688	261	81	44	27	11	5	2	1
	%	79.7	12.4	3.85	2.08	1.31	.48	.19	.09	.04
C	*n*	1688	358	83	5	1	—	—	—	—
	%	79.7	16.6	3.93	.24	—	—	—	—	—

SUMMARY

The slender glass lizard (*Ophisaurus attenuatus*) is one of six North American species in the genus; its range is much more extensive than those of the other five species combined. *Ophisaurus ventralis*, *O. compressus*, and *O. mimicus* occur in the southeastern United States and all three overlap *O. attenuatus*. *Ophisaurus ceroni* from the sand dunes of Veracruz, Mexico, and *O. incomptus* from near San Luis Potosí are virtually unknown. The six Old World species, recently assigned to a separate genus, *Pseudopus*, occur in eastern Europe, Asia Minor, Morocco, the eastern Himalayas, Burma, southern China, Formosa, and Borneo. The fossil record extends back to the Eocene in Europe and the Miocene in North America.

Because of secretive and elusive habits, the slender glass lizard has remained poorly known. Its habitat is tallgrass prairie, a fire subclimax. Many of these lizards are killed in prairie fires. Survival depends on escaping underground or living in marginal sites where bare rock, exposed soil, brush, and trees break the continuity of the grass cover.

On the University of Kansas Natural History Reservation where a population study was made, the population was extremely sparse when pastures were heavily grazed, i.e., up until 1948. After removal of livestock when the tract was set aside as a natural area, the population increased slowly but steadily. On a 7-hectare study area, averages of monthly capture-recapture ratios indicated that there were 519 lizards in 1965, 456 in 1966, and 712 in 1967. Their biomass was calculated as 1.93–3.01 kg per hectare during those years. After 1967 the population stopped increasing, and began a steady decline which has continued for 20 years. The reduction is correlated with habitat changes, as brush and trees replaced grass.

Female and immature slender glass lizards have a tan ground color, with a narrow black vertebral stripe. In adult males the tan dorsolateral areas develop white flecks and black speckling. These markings become more prominent with age and tend to form transverse bars. Also, the facial region is more heavily marked in adult males, and males grow to be 5% longer than females on the average. Relative tail length is about 4% greater in adult males than in adult females. Allometric growth causes gradual progressive changes in the proportions of the head and tail throughout life. Heads are relatively widest in hatchlings (7.46% of SVL), and narrowest in old females (4.73% of SVL).

Slender glass lizards are often diurnal, but sometimes crepuscular or nocturnal. Activity is much influenced by temperature and humidity. Much time is spent underground. Surface activity is elicited by warm summer rains. Body temperatures of those glass lizards that are active are often within the range 26°–30°C (extremes of 17.4° and 34.7°C). Hibernation occurs underground, usually in the tunnel systems of small mammals, within the area of the lizard's summer activities.

Each slender glass lizard tends to stay within a familiar area, but home ranges do not have well defined structure or boundaries. Adults cover larger areas than immatures, and males range more widely than females. The average home range was found to be 0.14 hectares in juveniles and 0.44 hectares for adult males.

Slender glass lizards find their prey partly by olfaction. They move slowly through the grass to find and stalk small animals, which are caught with a sudden lunge. Grasshoppers, crickets, and katydids make up the greater part of the food. Grasshoppers are especially prominent in the diet in late summer and autumn. Beetles and spiders also are important. Snails and small vertebrates are eaten occasionally. Vertebrates eaten include small frogs and young of small mammals taken from the nest.

The tail has important functions in locomotion and storage of fat. However, most glass lizards have broken and regenerated their tails by the time they are full grown. The tails are highly fragile because each vertebra has a fracture plane. When the lizard is grasped by the tail, fracture occurs, and the tail flips and wriggles with violent contractions that often distract the attention of a predator. A sudden scare may cause a lizard to flip off its own tail even though it has not been touched. Broken tails average about 13% (up to 50%) of the lizard's total weight, and the loss involves sacrifice of stored fat, and a handicap in locomotion that drastically reduces speed. Regeneration begins after about ten days and is most rapid in the first three months after the break. Nearly all regeneration is within the first year. The regenerated tail may attain 30% of the missing part, but in most cases considerably less.

Carnivorous mammals, hawks, and snakes are important predators on slender glass lizards. The red-tailed hawk was recorded as preying on glass lizards in 13 instances, and the copperhead in eight instances. The broad-winged hawk, yellowbelly racer, prairie king snake, ringneck snake, and raccoon were also recorded to prey on glass lizards, but their relative importance is not known. Other predators, including skunks, are suspected although specific records are lacking.

Mating occurs in May when adult males are most active. Testicular regression occurs in late May and early June. Females mature at three or four years of age, usually at lengths slightly greater than 190 mm (SVL). Approximately 60% of the females found in June were not gravid, but those that are gravid are more secretive, tending to remain underground. A biennial breeding cycle is suspected. Egg-laying usually occurs in the first week of July. Nests may be in cavities beneath flat rocks or in abandoned tunnels of small mammals (*Scalopus*, *Microtus*). The female coils around her eggs and remains with them throughout incubation, but is not active or aggressive in defending them against small predators. Clutches average 10.2 ± 0.47 eggs (range of 5–16, $n = 40$). Relative clutch mass in 20 clutches averaged 24.62% (11.9–44.7%). Incubation lasts seven to eight weeks. Hatchlings average 56.8 ± 0.30 mm SVL (50–63 mm) and weigh 1.23 ± 0.05 grams. Early growth is rapid, with gains a little more than 0.6 mm (SVL) per day. By the end of the first year the rate of increase is less than half that of the early weeks. At an age of one year the young average 125 mm SVL, a little more than half the adult length. At an age of two years they average about 185 mm. Three-year-old adolescents average 197 mm. Average adults are 233 mm SVL (males) and 223 mm (females). Maximum lengths in the local population were 264 mm SVL (males) and 244 mm (females). Growth continues throughout life, but is much slower in adults (1–2 mm per month) than in immatures. Glass lizards are relatively long lived. One was caught over a nine-year period and six others were known to have survived seven or eight years. The population of adolescents and adults was calculated to sustain an annual loss of about 40%, but loss was 56% for the egg stage and first year combined, and 50% during the second year.

In my 35-year field study, 2116 slender glass lizards were captured a total of 3353 times on or near the University of Kansas Natural History Reservation.

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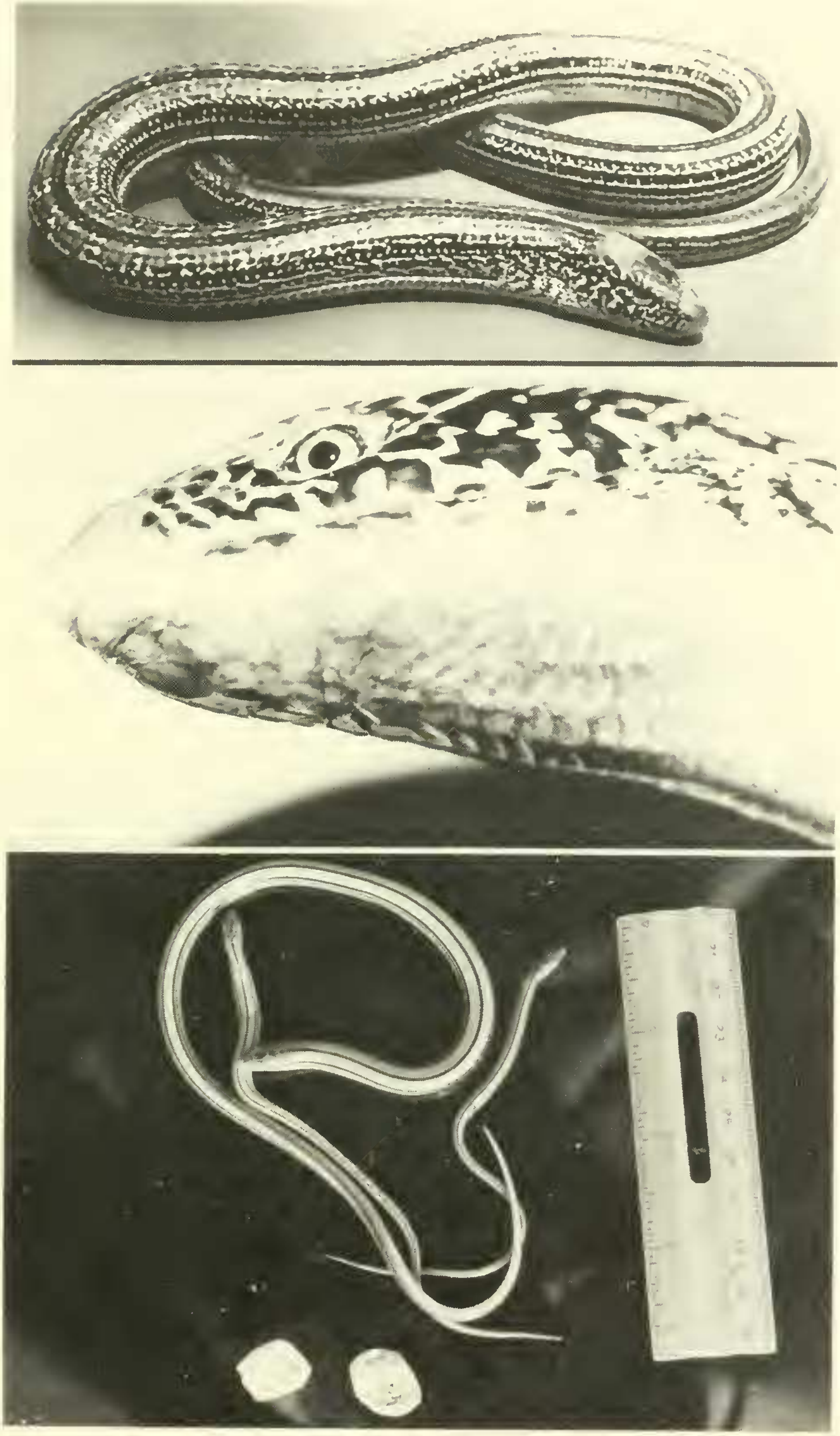

Plate 1. *Upper:* Large adult male western slender glass lizard, showing relatively blunt head, and dorsolateral area of body heavily speckled with black and white. *Middle:* Head of adult male western slender glass lizard, ventrolateral view showing heavily marked facial region. *Lower:* Adult female western slender glass lizard with two hatchlings and their collapsed egg shells.

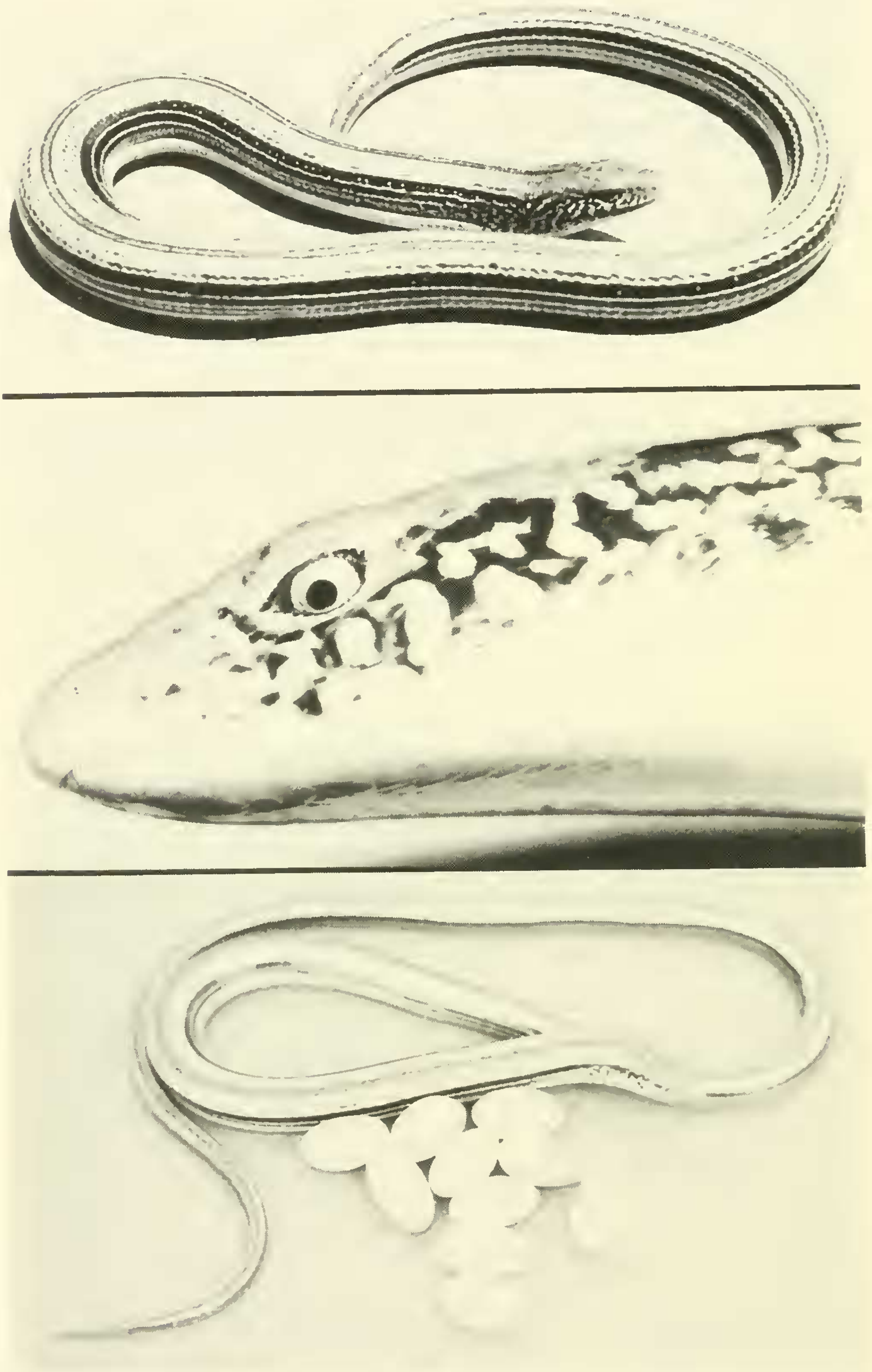

Plate 2. *Upper:* Large adult female western slender glass lizard showing relatively narrow head, and dorsolateral area sparsely dotted with black but no white. *Middle:* Head of adult female western slender glass lizard, lateral view, showing facial markings, chiefly on temporal and subocular regions, sparse on side of rostrum. *Lower:* Adult female western slender glass lizard with newly laid clutch of eggs.